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THE SEASONAL AND DIURNAL ACTIVITY OF THE FAUNA SAMPLED BY PITFALL TRAPS IN DIFFERENT HABITATS

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(With 4 Figures in the Text)

Twenty-four hour rhythms of activity are widespread in the animal kingdom (Calhoun 1944-46), so much so that it has been suggested (Harker 1958) that there is a basic twenty-four hour rhythm in the cells of all animals even if this is not shown in overt behaviour. A great deal of research has been undertaken to establish the nature of the 'clock' which enables rhythms to persist under uniform conditions and which keeps time even in poikilotherms subject to widely fluctuating temperatures, and a number of physiological models have been proposed (Harker 1958, Hastings & Sweeney 1957, Pittendrigh & Bruce 1957). Research on the mechanism of time-keeping has overshadowed the ecological implications of the rhythms and extrapolation from the laboratory to the field has only been made to show how far the experimental results are pertinent to the particular animal's natural mode of life. The only discussion of the rhythms shown by communities has been that of Park (1941).

Park argues, on theoretical grounds, that there is an evolution of communities from a primitive state in which activity is asymmetrical in the twenty-four hour cycle (or diel) to a more advanced state in which activity is symmetrically disposed around the diel. His argument may be paraphrased as follows: in community physiology, the unifying principle is that the available resources should be fully exploited, and a community which includes both nocturnal and diurnal animals is using the resources more efficiently than a community with a single phase of activity. Consequently, there is a development to the state where the total activity of the community is uniform throughout the diel, that is, where community activity is arhythmic despite rhythms of behaviour in the individual species which make up the assemblage. The idea is probably familiar to all animal ecologists as the well-known text book (Allee *et al.* 1949) provides its pictorial demonstration in human societies, a small village showing a rhythm of activity which follows the environmental change from day to night whereas in a city, activity is continuous throughout the twenty-four hours.

The hypothesis seems to be reasonable when applied to natural communities, but no field observations have been directed specifically to test its validity and it was for this reason that the present observations were begun. The most convincing test would be an estimate of the total activity of communities selected from the extremes of possible community range, comparing, for example, a raw quarry face with the climax woodland behind it. But to measure the total activity

of a rich community lies beyond the powers of a single investigator so that some limitation is essential in the definitions of activity and community.

In the present context energy expended in the exploitation of the resources of the community would be the best measure of activity, but that is impossible in the field, so recourse was had to locomotor activity. Locomotor activity of the population is susceptible to field sampling but it may be argued that a moving animal is, almost by definition, not exploiting the available food supply and that the process being sampled is the dissipation rather than the utilization of resources. But locomotion does reflect productive activity, for active searching is an essential part of food-gathering for most carnivores, while even for herbivores movement is generally from one food supply to another, an attempt to escape predation, or passage to a new niche in which to complete development. Similarly, a rich community is too complex a unit to be sampled in its entirety so that attention was confined to a part. The floor was selected as it is common to all terrestrial habitats and provides different levels of complexity; in woodland, a rich litter layer is provided together with large fungi, broken branches and other debris which furnish the primary habitat units for animal communities (Elton 1949); in grassland, both the litter and the debris are absent and the primary habitats are restricted to plants of the herb layer and the products of their decay. Further, as stressed by Elton & Miller (1954), all organisms contribute to the energy relationships of the floor, and many, which would not normally be classed as ground-dwelling forms, come to the ground as transients. The floor fauna was not sampled in its entirety for the pitfall trapping methods used were not suitable for vertebrates, but it was felt that an answer for an arbitrary proportion of community activity would be better than no knowledge at all and the gaps could be filled in later.

SAMPLED AREAS AND SAMPLING METHODS

Park deduced from his hypothesis that the degree of symmetry of activity would give an estimate of the 'complexity' of a community, thus providing a standard of measurement for a quality which can be appreciated intuitively but which is difficult to define. However, in this investigation this useful yard-stick could not be used, as the symmetry of activity would not be known until the investigation was completed. Areas were therefore selected on the basis of differences in apparent complexity, and the first need was to determine whether the areas did differ in the richness of their floor fauna. To do this simple pitfalls were run for a year, and this had the added advantage that the traps, being cheap, could be replicated in each area, whereas the more elaborate pitfalls it was proposed to use for separating the fauna into nocturnal and diurnal components would be too expensive to duplicate. In this way, the simple traps could be used to compensate for sampling errors in the time-sorting traps.

Three areas were chosen on the University Farm near Shinfield, Berkshire; a wood (Rushy Mead), open scrub (Mill Copse), and a newly seeded ley (Mill Field). Rushy Mead (Nat. Grid Ref. 752692) is a copse of about 10 acres on a gravelly

loam. It is bisected by a ride separating alder coppice to the north-west from mixed oak and hawthorn to the south-east. The oak canopy is high and thin, allowing the invasion of a mixed ground flora, but gives way to dense hawthorn with a pure litter layer beneath. From a forester's point of view the wood has been badly neglected with the result that there is much dead wood in various stages of decomposition and the ride provides a margin from which invasion of the ground vegetation can take place, thus diversifying the type of floor cover even more. The whole area is low-lying and liable to floods and Rushy Mead is virtually isolated from the surrounding fields by an encircling drainage ditch.

Mill Copse (743680) is an area of some $2\frac{1}{2}$ acres bounded by a windbreak of Douglas fir and a hawthorn hedge. A few small trees of fir and oak are scattered about the copse but the main vegetation is provided by clumps of briar, bramble and privet, the intervening spaces being dominated by clumps of cocksfoot and hogweed with the moss *Pseudoscleropodium purum* (Hedw.) at the bases of the tussocks.

Mill Field is adjacent to Mill Copse and was in its first year as a ley after being seeded under barley the preceding spring. When the investigation began in February 1952 the barley stubble was still conspicuous. The field was subject to the normal farm routine, being cut for hay and intensively grazed, the grazing being controlled by movable electric fences.

In each area, three pitfall traps were sunk. Each trap was 1 m in circumference and 8 cm deep, with the base wider than the mouth so that the sides of the trap sloped outward from the mouth and thus provided no foothold which could be used by an animal to avoid capture. To prevent escape from the trap and predation within it, the catch was inactivated by commercial grease-banding material (Stictite). This was smeared on to split Bakelite rings which were left in the trap while in use and removed to the laboratory between samples, when the catch could be picked out under a binocular microscope. The traps were provided with an aluminium lid to exclude rain and debris, the lids sitting on a centre post and held about 5 cm above the level of the ground. The trap could be closed by pushing down the centre post when no samples were required. The bottom of the trap was made of phosphor-bronze gauze which permitted free drainage but excluded soil animals.

The traps were not placed at random in each general area but were sited to sample the main types of habitat. Thus in Rushy Mead, trap A was under oak with a good litter layer which did not preclude the invasion of plants of the field layer, chiefly *Chamaenerion angustifolium* (L.), *Gallium* sp., *Glechoma hederacea* L. and nettles; trap B was under a dense hawthorn stand with a thick litter layer and no ground vegetation; and trap C was under coppiced alder with nettles, *Filipendula ulmaria* (L.) and *Mercurialis perennis* L. as ground cover. In Mill Copse, traps A and B were placed at different distances from clumps of bushes, and trap C in the fir windbreak; in Mill Field, traps A and B were placed at random as the field was uniform and trap C about 3 ft away from the hawthorn hedge, and opposite trap C of Mill Copse.

To determine the distribution of activity throughout the diel, pitfall traps were used which incorporated a mechanism which sampled the twenty-four hours in six separate periods. The mechanism has been fully described elsewhere (Williams 1958) and consists, briefly, of a gramophone turntable which rotates six pots beneath a funnel. Each pot receives the catch for a definite period of the day, the periods employed in the present investigation being: 1—from midnight to one hour before sunrise; 2—from one hour before sunrise to one hour after sunrise; 3—from one hour after sunrise to noon; 4—from noon to one hour before sunset; 5—from one hour before sunset to one hour after sunset; 6—from one hour after sunset to midnight.

One trap was placed in Rushy Mead and one in Mill Copse, the Mill Field site being omitted for reasons given below. Both traps had the same circumference and the two traps were operated simultaneously for 24 h at a time. Sampling was at fortnightly intervals approximately, but as this programme could not be rigidly followed, twenty-three samples were taken from July 1956 to June 1957, and these were distributed throughout the year as evenly as possible. About 5 yd away from each trap a recording thermohygrograph was set up under a wooden shelter. These were standard meteorological instruments with a hair hygrometer and bi-metal strip and the effective responsive elements were thus about 8 cm above ground level. Accurate measurements of conditions on the floor were not taken, as the trapped fauna originated in a variety of places other than the floor itself.

POPULATION LEVELS AND PATTERNS OF ACTIVITY

Park (1941) showed that the proportion of the twenty-four hour cycle utilized by human societies was directly related to the number of people in the social unit. Implicit in the demonstration was the assumption that with increasing numbers went an increase in diversity of occupation which allowed increasing symmetry of activity. In terms of the animal community, these two aspects of complexity would be represented by the number of individuals and the number of species, the latter representing the diversity of human occupation. This second aspect cannot be analysed here, as complete identification of the 14 000 invertebrates caught has not yet been made. Cursory examination shows that the larger the numbers of animals caught the greater is the number of species represented, but beyond that simple statement no precise analysis is possible; the present paper is therefore restricted to total numbers. The catch is mainly of arthropods, together with a few annelids and molluscs, and among the arthropods Collembola, Coleoptera and Acarina predominate.

The simple pitfalls were in operation concurrently from February 1952 to January 1953 inclusive, and samples were taken every 4 weeks, the traps operating for a week at a time. The numbers of invertebrates caught in each trap, after correction for the effect of Stictite (Williams 1958), are given in Table 1, together with the analysis of variance of the data transformed to log $(n+1)$. The differences between the traps in any one area are significant so that, for example, in Rushy

Mead the trap under oak was more productive than the trap under alder, but over-riding this variation the differences between areas is also significant. The *t* test applied to the area means shows that Mill Field with a mean capture per trap of 96 does not differ from Mill Copse with a mean capture of 91, but Rushy Mead (mean 167) is significantly more productive than either. Mill Copse differs from Mill Field in the presence of numerous bushes, and it was supposed, when the areas were chosen, that this might be reflected in the ground

Table 1. *The adjusted totals of the numbers of animals caught per simple trap for each sampling week*

Sampling week beginning	Rushy Mead			Mill Copse			Mill Field		
	A	B	C	A	B	C	A	B	C
6 February	47	32	77	15	21	31	63	20	62
5 March	100	83	124	49	90	50	103	57	77
2 April	93	91	127	74	87	56	119	37	47
30 April	210	181	194	118	152	84	169	70	181
28 May	254	216	235	192	232	203	125	106	249
26 June	571	233	233	158	233	165	155	110	412
23 July	373	156	133	99	144	95	65	115	226
20 August	267	159	148	158	135	127	102	42	121
17 September	300	129	148	98	87	75	89	83	91
15 October	341	109	244	63	62	45	77	73	77
12 November	169	62	167	39	50	27	52	82	33
10 December	102	48	118	55	69	51	57	51	58
6 January	96	42	95	36	24	19	26	26	45
Total	2923	1541	2043	1154	1386	1028	1202	872	1679

Analysis of variance $\log_{10}(n+1)$

	d.f.	*V*	*F*	Significance
a Sampling periods	12	0·5290	$a/f = 25{\cdot}311$	HS
b Areas	2	0·8943	$b/c = 6{\cdot}293$	S
c Traps within areas	6	0·1421	$c/f = 6{\cdot}799$	HS
d Periods × areas	24	0·0268	$d/e = 1{\cdot}418$	ns
e Periods × traps within areas	72	0·0189		
f = (*d*+*e*)	96	0·0209		
Total	116			

ns = not significant; S = significant ($P = 0{\cdot}05$); HS = highly significant ($P = 0{\cdot}01$)

fauna by supplying species which were only present as transients; the sampling periods were made rather long to increase the chances of trapping such transients. It is clear that these migrating forms do not add appreciably to the ground fauna in Mill Copse, possibly because the bushes do not form a canopy from which caterpillars and other larval forms can drop to all parts of the floor when pupating.

The sole aim of the preliminary sampling by simple pitfalls was to determine whether the three areas differed in the population levels of active animals and it is clear that the two Mill sites do not. For the analysis of diurnal and nocturnal faunas, therefore, Rushy Mead may be compared with either Mill Copse or Mill Field. The time-sorting traps were placed in Rushy Mead and Mill Copse as Mill Field was a troublesome area to work in, cows sometimes damaging the traps.

The number of invertebrates caught during each sampling period in the time-sorting pitfalls is given in Table 2. The numbers have been adjusted to compensate for the bias introduced by the presence of a funnel in the trap (Williams 1958) and aquatic insects which were caught have been excluded as these are not normal constituents of the floor fauna but are attracted to the traps by the perspex lids.

In this instance, the total catch for the year was virtually the same in Rushy Mead and Mill Copse, the adjusted totals being 1231 and 1189 respectively, but

Table 2. *The adjusted numbers of invertebrates falling into the time-sorting pitfall traps*

RM = Rushy Mead; MC = Mill Copse; h = duration of the period in hours. The periods are numbered as in the text (p. 4).

	Periods																	
	1			2			3			4			5			6		
	RM	MC	h	RM	MC	h	RM	MC	h	RM	MC	h	RM	MC	h	RM	MC	h
27 July	6	2	3	9	2	2	23	23	7	12	28	7	5	3	2	9	2	3
3 August	3	4	3·5	5	0	2	5	11	6·5	21	17	7	1	11	2	7	5	3
16 August	10	3	4	2	4	2	17	11	6	12	35	6·5	12	6	2	21	4	3·5
11 September	7	1	4·5	1	1	2	15	8	5·5	13	22	5·5	11	6	2	10	6	4·5
21 September	21	9	5	3	1	2	7	3	5	4	3	5	3	2	2	24	4	5
18 October	5	2	5·5	2	0	2	5	2	4·5	9	17	4	3	2	2	13	4	6
1 November	6	3	6	1	3	2	2	5	4	9	12	3·5	5	7	2	5	5	6·5
17 November	7	6	6	1	1	2	1	0	4	2	0	3·5	6	7	2	10	3	6·5
1 December	3	1	6·5	1	1	2	2	0	3·5	1	0	3	3	3	2	3	4	7
14 December	6	1	7	4	0	2	2	2	3	2	0	3	4	0	2	7	4	7
4 January	5	5	7	4	1	2	1	2	3	1	1	3	0	0	2	2	3	7
17 January	14	0	7	9	1	2	7	2	3	12	0	3·5	1	3	2	10	8	6·5
31 January	8	2	6·5	7	0	2	8	0	3·5	7	1	4	0	1	2	8	3	6
14 March	18	6	5	3	5	2	4	13	5	10	12	5	3	1	2	16	7	5
21 March	7	5	5	3	8	2	11	18	5	21	18	5	6	8	2	9	3	5
5 April	30	1	4·5	7	3	2	19	30	5·5	21	17	6	9	10	2	14	13	4
12 April	8	14	4	6	5	2	19	31	6	19	30	6	5	7	2	8	4	4
26 April	5	5	4	5	5	2	3	10	6	9	45	6·5	3	3	2	5	0	3·5
10 May	10	6	3·5	2	0	2	9	41	6·5	38	46	6·5	6	5	2	12	9	3·5
22 May	6	5	3	3	5	2	7	36	7	20	48	7	10	15	2	7	11	3
4 June	14	10	3	7	10	2	18	15	7	51	33	7	9	19	2	20	16	3
20 June	6	3	2·5	3	4	2	11	35	7·5	24	26	7·5	8	4	2	7	3	2·5
28 June	6	7	2·5	2	5	2	19	30	7·5	27	27	7·5	8	7	2	22	6	2·5
Total	211	101		90	65		215	328		345	438		121	130		249	127	

this is the type of experimental error to be expected when single traps are used. It results from the positioning of the traps, for in Mill Copse, where the general level of activity is low, the trap was carefully placed on the site of the simple pitfall which had given the highest yield, whereas in Rushy Mead the single trap was placed at random in a convenient spot.

The totals in Table 2 suggest that the active fauna in Mill Copse is predominantly diurnal, the day-time catch represented by periods 3 and 4 being about three times the nocturnal catch obtained by summing periods 1 and 6. The ratio of day to night captures in Rushy Mead is much nearer unity, viz. 1:1·2. The twilight catches (periods 2 and 5) were approximately equal in the two areas and contribute

16% of the total in Mill Copse and 17% in Rushy Mead. However, the periods change in duration throughout the year as their limits are determined by the time of sunrise and sunset, so a better comparison of the two areas is obtained by comparing the rates of capture. The unit used for rate of capture has been the number of animals which would be caught in 10 h, this giving a figure of convenient magnitude, and in Fig. 1 the results for the six periods in the two areas are displayed in the form of a radial histogram. It can be seen that the pattern of activity in Rushy Mead very nearly approaches complete symmetry, whereas

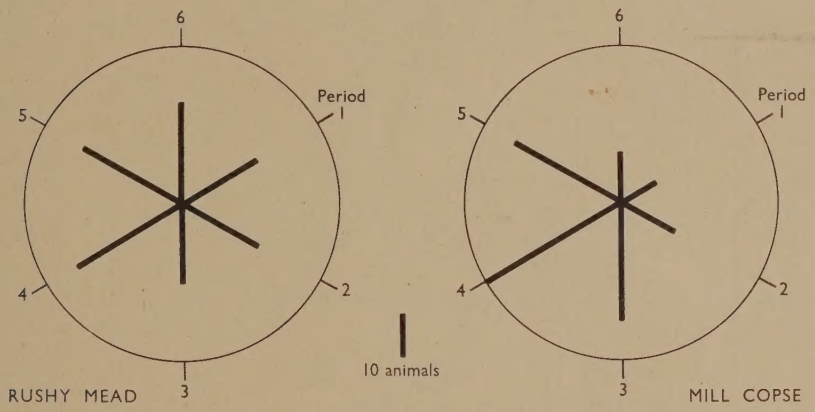

Fig. 1. The estimated numbers of invertebrates which would be caught in sampling periods of 10 h duration. The periods are numbered as in the text, period 1 beginning at midnight and period 4 at noon.

activity in Mill Copse is markedly asymmetrical. As Rushy Mead has also been shown to have the richer fauna, the observations confirm Park's hypothesis.

SEASONAL VARIATION

The high value of the captures for Rushy Mead in comparison with Mill Copse and Mill Field may be due to either of two factors. The presence of a distinct canopy and litter layer might buffer the climatic fluctuations in Rushy Mead, thus allowing a large annual total to accumulate from relatively small individual samples, or the litter layer might provide an extra industry which permits exploitation at a higher population level. To discriminate between these two alternatives it is worth while examining the annual fluctuation in the catch after reducing the figures to a common base-line. This has been done in Fig. 2 where the captures for each sample are shown as a percentage of the annual mean for the area, the comparison being between the simple pitfalls in Rushy Mead on the one hand and those in Mill Field and Mill Copse on the other. It is clear that the amplitude of fluctuations is the same in both instances, for although the detailed forms of the curves differ the departures from the common base-line are equal for both curves. This would suggest that the higher population in the wood is not

the result of a smoothing out of seasonal fluctuations, for these are relatively the same in the two types of habitat. The same absence of buffering can be shown at the individual trap level by attempting to correlate the total number of animals caught per trap with the amount of variation shown by each trap throughout the year, for if larger catches are the result of damped fluctuations then there should be a negative correlation between numbers caught and variation. The annual

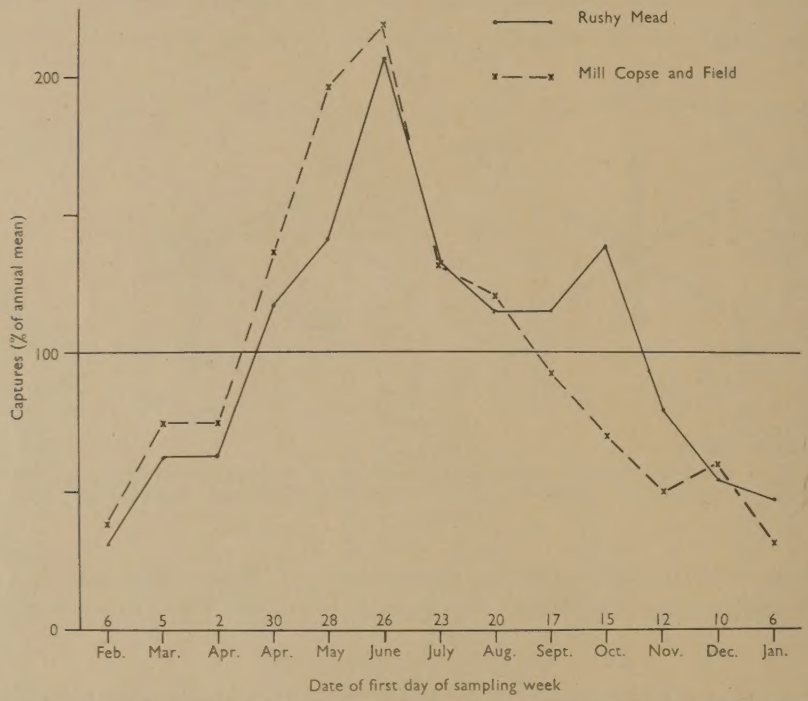
Rushy Mead
Mill Copse and Field
Captures (% of annual mean)
200
100
0
6 5 2 30 28 26 23 20 17 15 12 10 6
Feb. Mar. Apr. Apr. May June July Aug. Sept. Oct. Nov. Dec. Jan.
Date of first day of sampling week

Fig. 2. The annual fluctuations in the numbers of animals caught within and outside Rushy Mead by the simple pitfall traps compared by reducing each sample to a percentage of the annual mean for the sampled area.

variation of the captures by traps with different yields can again be reduced to a common baseline by using the coefficient of variation (100 × standard deviation/mean), and the value of r, the correlation coefficient, obtained between the number caught per trap and the coefficient of variation for each trap is +0·08, which is not significant. The larger catches in Rushy Mead are thus not due to a simple buffering effect provided by the wood but to the presence of the litter layer which gives a further source to exploit. This is supported by consideration of the sites of the simple traps, for outside Rushy Mead the highest catch is given by Mill Field trap C which lies in the litter from the hawthorn hedge and is the only trap which does so. That this high value is not the result of shelter provided by

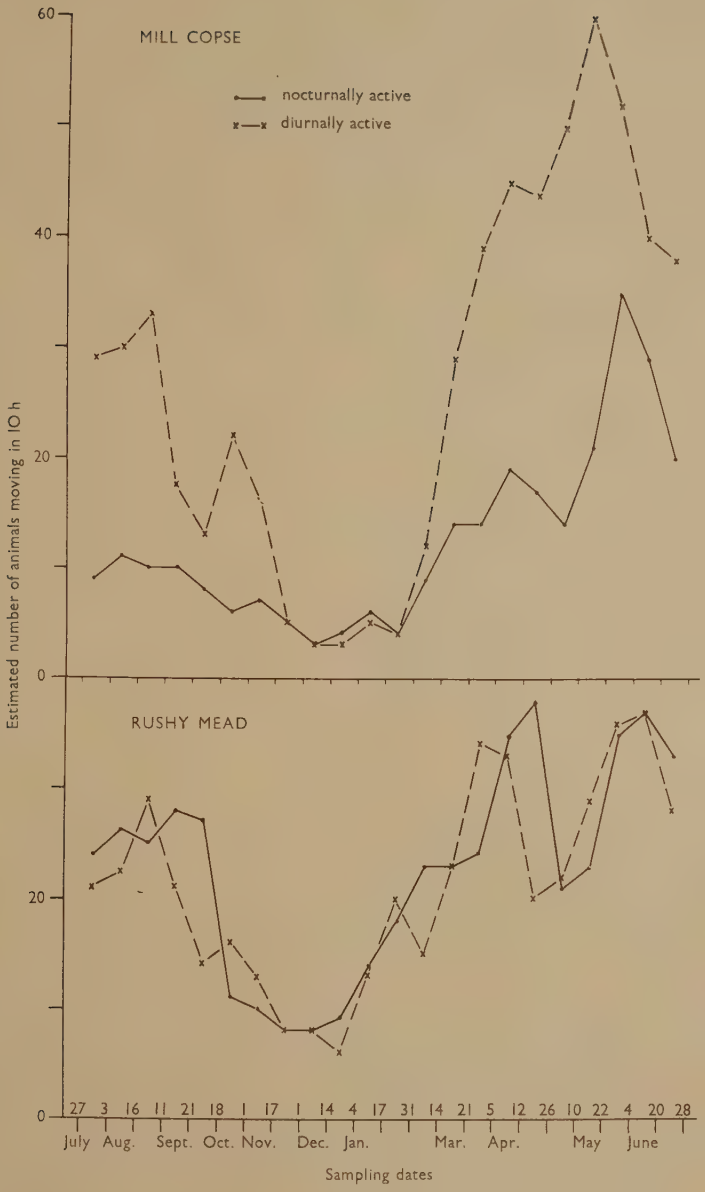
MILL COPSE
nocturnally active
diurnally active
RUSHY MEAD
Estimated number of animals moving in 10 h
60
40
20
0
20
0
27 3 16 11 21 18 1 17 1 14 4 17 31 14 21 5 12 26 10 22 4 20 28
July Aug. Sept. Oct. Nov. Dec. Jan. Mar. Apr. May June
Sampling dates

Fig. 3. The annual variation in diurnal and nocturnal activity in Mill Copse and Rushy Mead. Nocturnal activity is displayed as the running mean of periods 1, 2 and 6, diurnal activity by the running mean of periods 3, 4 and 5.

the hedge, is shown by comparison with Mill Copse trap C, which shares the hedge but not the litter and gives a catch significantly smaller than Mill Field C.

Fig. 1 represents the mean of a year's sampling and it is of interest to examine the change in the distribution of diel activity throughout the year. This is displayed in Fig. 3 after a number of restrictions have been imposed on the original data obtained from the time-sorting traps. The sampling errors are large as only one trap was in operation in each area and the catch of each trap was further subdivided into six periods. The unavoidable sampling fluctuations have been smoothed in the following way. Examination of the annual cycle for individual

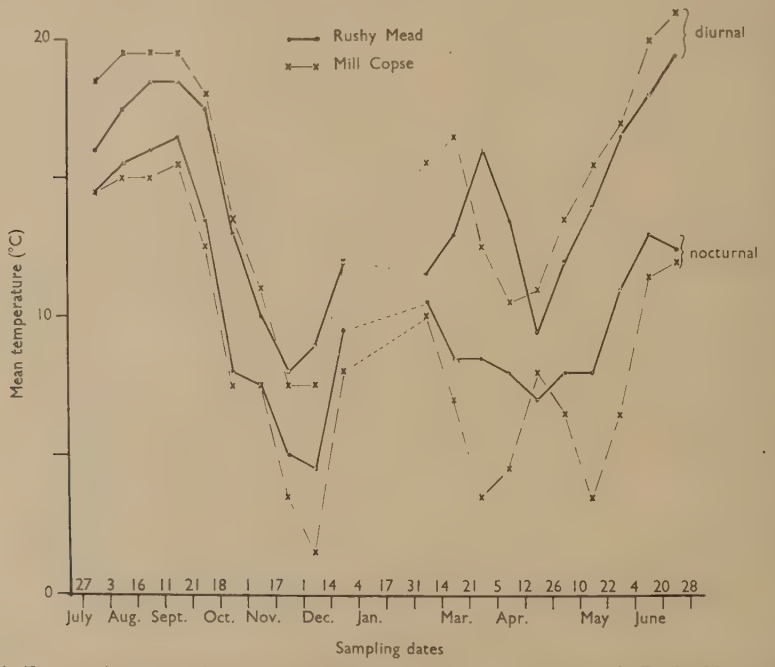
Rushy Mead
Mill Copse
diurnal
nocturnal
Mean temperature (°C)
20
10
0
27 3 16 11 21 18 1 17 1 14 4 17 31 14 21 5 12 26 10 22 4 20 28
July Aug. Sept. Oct. Nov. Dec. Jan. Mar. Apr. May June
Sampling dates

Fig. 4. The running mean of the mean nocturnal and diurnal temperatures in Rushy Mead and Mill Copse.

periods shows that periods 1, 2 and 6 share the same general features and can be amalgamated to give a nocturnal fauna, while periods 3, 4 and 5 are similar and give a diurnal fauna; the faunal composition of the periods confirms this division. In Fig. 3, therefore, the periods are combined in this way, and the running means are plotted. In parenthesis it may be mentioned here that the pitfall catches do not give any indication of a definite crepuscular fauna which is qualitatively unique. Rather, period 5 is an extension of period 4 with a little overlap with period 6, and period 2 is similarly intermediate between periods 1 and 3, though sharing more the characteristics of period 1. The linking of the dawn figures with the nocturnal fauna and the dusk figures with the diurnal fauna is the reverse

of that suggested by Park (in Allee *et al.* 1949), but the physical factors at dawn, other than light-intensity, are those of the preceding night, as there is a lag in the rise of temperature and fall of humidity behind the increasing light.

In confirmation of the preliminary sampling, Fig. 3 shows that total locomotor activity on the floor varies widely through the year, being low in winter and high in summer, and that the annual fluctuations in Rushy Mead are not significantly damped when compared with Mill Copse. From November to January activity is low in both areas and at the same general level by day and by night. From March onward total activity increases in both areas, but in Mill Copse this is mainly by increase in diurnal activity, whereas in Rushy Mead diurnal and nocturnal activity increase equally and remain remarkably similar. Again the possibility exists that the more uniform distribution of day and night activity in Rushy Mead is the result of the smoothing effect of the canopy on the fluctuations of physical factors, but that this is not so can be seen by comparing Fig. 3 with Fig. 4, which shows the running mean of the mean diurnal and nocturnal temperatures for the two areas. It will be seen that the ambient temperature does not fluctuate between such wide limits in the wood as in Mill Copse, but the temperature differences are not commensurate with the activity differences. To obtain a numerical value of the relationship between the smoothing of weather conditions and the smoothing of activity, correlation coefficients were calculated for each area, the two variables being the discrepancy between the nocturnal and diurnal temperatures and the difference between the level of activity by day and by night. In both cases the value of r was not significant, being $+0{\cdot}401$ in Mill Copse and $-0{\cdot}242$ in Rushy Mead. Similarly, in the raw data, no correlation is found between temperature during any one period and the rate of capture for that period.

DISCUSSION

The preliminary trapping shows that locomotor activity in the wood is greater than in the other areas sampled, and that this high level of activity is associated with the presence of a definite litter layer. Activity in the wood is symmetrically displayed throughout the twenty-four hour cycle whereas activity in the poorer community is markedly asymmetrical. Within the limits imposed by studying only a part of the total community this supports the deductions made by Park (1941).

The difference in symmetry is not a simple result of smoothed weather fluctuations, and a number of questions are posed which it is hoped to answer in future qualitative analysis. If one may extrapolate from Park's illustration of activity in human society, symmetry is probably most nearly approached in an evolved society which is at war. Under such conditions, industries directly affecting the war potential must be kept in continuous production, which can be done by using a shift system in which the individuals manning a machine are replaced throughout the diel while the machine works continuously. Does a shift system operate in the wood, which also approaches symmetry in the distribution of activity, and in which the basic industries, *e.g.* decomposition of litter, may also be regarded as

continuous throughout the day and night? Is the symmetry the sum of arhythmic activity by individual organisms, the result of a shift system in which members of a single species alternate, or the result of a shift system to which different species contribute? The last alternative certainly operates in Rushy Mead but further work is needed to discriminate between the other two possibilities.

The litter provides the substrate upon which such a shift system can work but periodic activity also implies periodic rest and here again the wood is better provided for than the scrub. In Rushy Mead, not only does the litter itself provide shelter but in addition there are abundant retreats. The wood is not exploited in any way and is well supplied with dead wood lying on the ground and standing erect, held by the tangle of branches; the ride provides a herb layer, as do stretches where the canopy is thin; while the soil is loosened by the activity of earthworms and other burrowers. The floor animals can find shelter by retreating upwards or downwards or by remaining in the litter.

Symmetry also poses a question in physiology. All the animals included in the above results are poikilothermal and their activity is dependent on temperature. The mean temperature at night in Rushy Mead is some 2 to 6° C below that by day but the respective active faunas are equal. This would suggest that the temperature responses of the nocturnal component of the fauna differ from those of the diurnal component or that the total nocturnal population is higher than the diurnal population providing a larger reservoir of animals with the same temperature relations.

The maintenance of symmetry throughout the year is remarkable when it is remembered that the trapped population is a very mixed one, each species having its own cycle of abundance and its own characteristic response to varying physical factors. That the sum of these separate activities should give rise to symmetry, and that the degree of symmetry is deducible from theoretical consideration of the possible physiology of communities, suggest that the community is an entity.

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SUMMARY

1. The floor of a wood is shown to yield higher pitfall captures than either an open scrub or a ley, and this is considered to be due to the presence of a distinct litter layer.

2. Distribution of locomotor activity, as measured by pitfalls, is more uniform throughout the twenty-four hour day-night cycle in the wood than in the scrub. This difference is not simply the result of the damping of climatic fluctuations in the wood, but is again related to the litter which provides extra food and extra retreats during periods of inactivity.

3. It is concluded that these results support the hypothesis that more complex communities have a more symmetrical disposition of activity than simpler communities.

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THE BIONOMICS OF THE WOOD CRICKET, *NEMOBIUS SYLVESTRIS* (ORTHOPTERA: GRYLLIDAE)*

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(With 7 Figures in the Text)

In 1949 Richards (1952) rediscovered *Nemobius sylvestris* (Bosc) in oak leaf litter in south-east Devon, confirming Parfitt's record (1882). In 1952 a detailed study was undertaken of the bionomics of this insect. The concept of a 'community' is a nebulous idea. A satisfactory description in quantitative terms is hardly possible because the number of variables is so large. In this complexity, however, there is a unit which is susceptible to present-day techniques, namely the species population. Description of a population in statistical terms is an essential preliminary to a serious consideration of its biology and of its relationships with other animals in the same habitat. This study attempts to translate into quantitative terms some selected variables which act upon, or occur within, the *Nemobius* population.

SITES AND METHODS

Three sites were chosen using the level of the population and the depth and uniformity of the litter as criteria. Included here is a general description of these sites; a more detailed study is given later.

Bicton (Grid Reference 30/075856). This site lies in south-east Devon to the west of the River Otter along the edge of a bank which runs from Bicton Church to Otterton village. In April 1954 the deep accumulation of litter was burnt so that work had to be discontinued.

Harpford Wood (Grid Reference 30/1090). This wood, mainly of oak and beech with larch and spruce stands, lies approximately 3 miles north-west of Sidmouth and 15 miles east of Exeter on the west side of the escarpment which runs north-south along the east bank of the Otter. The two areas lie on the north side of the railway running through the wood. Harpford 1 is at track level. The ground layer is composed, almost entirely, of *Pteridium* and *Lonicera* with occasional tufts of *Luzula*. There is a deep layer of litter characteristically of oak and beech leaves. Harpford 2 lies 150 m west of Harpford 1, at the top of an embankment. It resembles Harpford 1 but the litter layer is less deep and occasional patches of moss suggest that it is damper.

Quantitative sampling was carried out at Bicton from February 1953 to March 1954, at Harpford 1 from February 1953 to August 1955, and at Harpford 2 from June 1954 to August 1955. At each site twenty-five quadrats, each of 0·1 sq. m, were placed at random in a total sample area of 250 sq. m. The quadrat employed was 25 cm deep and resembled a box with top and bottom missing, so that pre-

* Part of a thesis submitted to the University of London for the Degree of Doctor of Philosophy.

mature escapes were minimized. Each site was normally sampled once a month but the frequency of visits was increased to three a month during the period of hatching.

The method comprised two distinct operations. All the visible specimens of *Nemobius* were first collected in 3 × 1 in. collecting tubes and preserved in 70% alcohol. The leaf litter was then removed from the quadrat and placed in sealed tins. In the laboratory the litter was placed on a sieve in a Tullgren funnel and the predatory species were extracted and preserved in 70% alcohol.

It is difficult to assess the efficiency of this type of sampling method in the field, but every precaution was taken to ensure that once the quadrat had been placed in position the chances of escapes were reduced to a minimum. The quadrat's sides prevented premature escapes, and animals which attempted to climb the sides were removed. The bottom edges of the quadrat were sharpened so that when firmly placed in the litter, it cut down into the soil beneath. On the infrequent occasions when the quadrat hit a large stone there might possibly have been escapes under the edges. When the litter was disturbed, *Nemobius* made short characteristic hops which enabled specimens to be seen and taken by the collector. After the litter had been removed from the sites, individuals which had been overlooked were either collected from the litter on its transference to the Tullgren funnels or separated from the litter during the gradual process of desiccation. The highest number of specimens collected by either of these methods never exceeded 5% of the total collection, and normally only one or two individuals appeared to have been missed by the hand sorting technique. The first, second and third instars were, however, liable to be overlooked on account of their small size.

THE LIFE CYCLE

Gabbutt (1958) describes the instars of *Nemobius* and the method by which they were separated. A head-width measurement was used, and the resulting polymodal distribution was analysed by Harding's method (1949). Later instars could be sexed and separated on morphological grounds so that all individuals could be allotted to a particular stage. It was possible, therefore, to estimate the density per square metre of each instar in a monthly collection.

The composition of the monthly collections at the three sites is illustrated in Fig. 1. The initial field collection of first instars was made at Harpford 1 on 26 July 1953. The absence of this nymph from the preceding collections suggests that hatching must have occurred between 22 June and the former date. The second, third and fourth instars are present during the months of August, September and October. The majority of the nymphs over-winter as fifth instars, although a few sixth instars were present. Growth in the population was at a standstill in winter and recommenced in May, when mainly sixth instars were present. The remaining sub-adult instars were present in June, July and August. Adults were present from August to October and finally disappeared in November.

A similar cycle of events can be followed for the nymphs which appeared in June 1954. This generation can be traced through its pre-winter development up to the

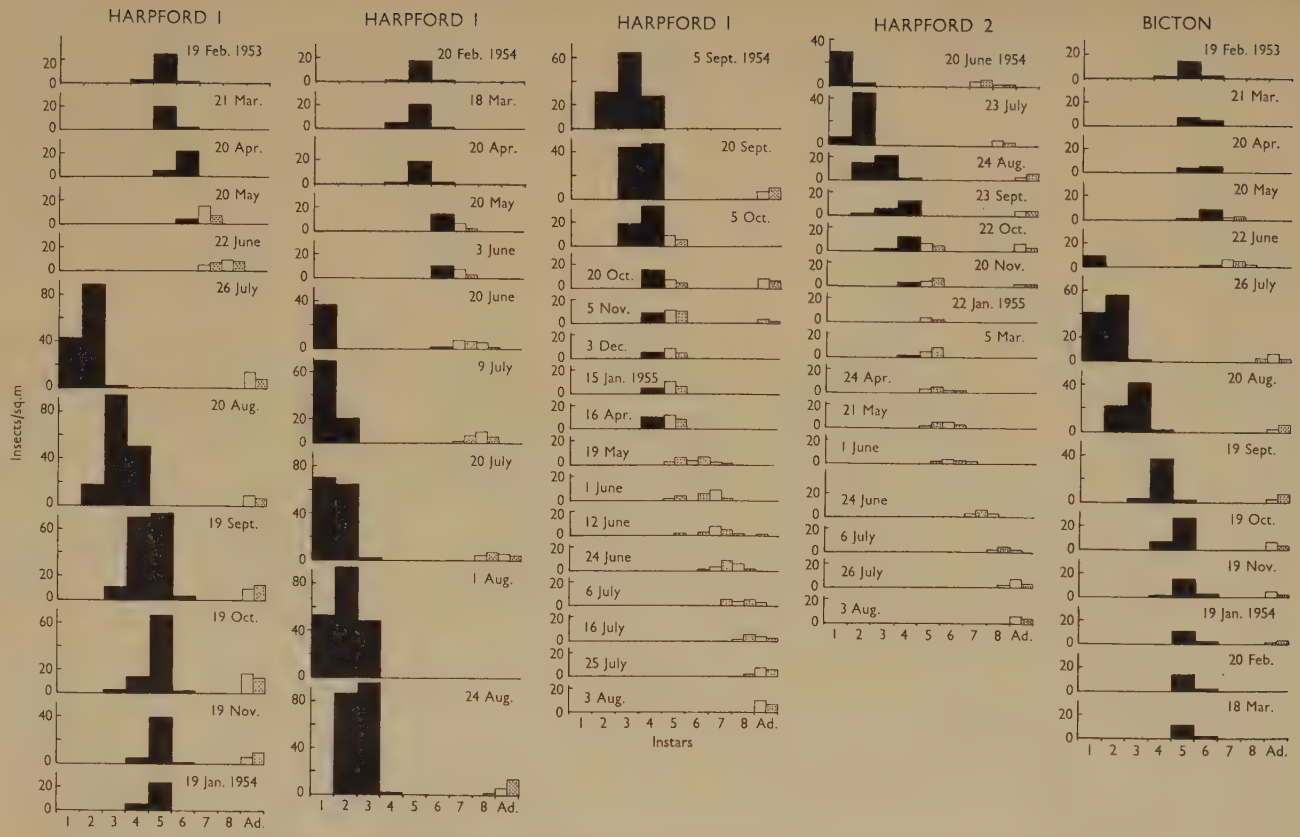

Fig. 1. The density of *Nemobius sylvestris* at the three sites. Black, unsexed nymphs; white, males; stippled, females. Adults were not collected on 1 August and 5 September 1954.

over-wintering fifth instar. Post-winter development took place from May onwards and the insect matured later in the year. Similar conditions prevailed at Harpford 2 and Bicton.

The two-year life cycle may be summarized as follows. Eggs laid during the summer and autumn of Year 1 over-winter and hatch in June and July of Year 2. The first five instars are present during the remainder of that summer and autumn; growth then ceases and the majority of the nymphs over-winter as the fifth instar. In the spring of Year 3 growth recommences and the insect reaches maturity in July and August. Fig. 1 shows that a number of generations coexist.

The fifth to eighth instars and the adults (Fig. 1) collected at Harpford 1 over the period February to August 1953 represent a generation which was initially laid in 1951. Henceforth this will be referred to as the 1951 generation. The eggs of this generation hatched in the summer of 1952 and the nymphs over-wintered to mature in the summer of 1953. Two other generations were present at this site: the 1952 generation as eggs in that year, as nymphs in 1953 and as adults in 1954, and the 1953 generation as nymphs in 1954 and as adults in 1955. The 1953 generation is, therefore, the offspring of the 1951 generation.

At Harpford 2 the 1951 and 1952 generations were present, and at Bicton the 1952 and 1953 generations were present.

The following general picture can be reconstructed of the density changes which take place during the course of the life cycle. The peak population follows hatching in July or August. This peak refers to the highest density calculated from the samples and not to the actual density peak. For instance, 408 and 406 individuals were collected on 20 August and 19 September respectively at Harpford 1, but the actual peak density must have occurred between these dates. The sudden build up in the population and the distribution of the instars in the collections indicates that the period of hatch must be comparatively short: from 4 to 8 weeks. The highest mortality occurs over the period from July to November, there being no evidence of nymphal dispersion; it mainly affects the first five instars, mortality amongst the over-wintering nymphs and adults being remarkably low. Harpford 1 supported the highest density of *Nemobius*, the peak population being 163 and 196 individuals sq. m for the 1952 and 1953 generations respectively. The peak density at the other two sites was lower. The adult density, also at Harpford 1, tended to be consistently higher.

The life cycle described agrees with that suggested by Syms (1938) and Richards (1952). Chopard (1951), however, reports that in France the life cycle is completed in 1 year. The adults appear in July and the eggs are laid almost immediately. These hatch after 2 months, and a period of growth follows before the nymphs over-winter to mature the following summer. Rober's (1949) description can be similarly interpreted. Both authors, however, make statements which are incompatible with a strictly one-year cycle. Rober (1949) states that 'spending the winter in the egg cannot be ruled out in view of the late hatching of the eggs' and his observations further show (October 1948) that 'freshly emerged young nymphs occurred, also nymphs of medium size, a small number of older nymphs and a

larger number of adults'. Chopard (1951) remarks 'in a mild winter many adults hibernate and finish laying their eggs in the spring *for one finds* [my italics] new nymphs hatching in July'. Professor Komarek (personal communication) in Prague describes a life cycle identical with that described here, but adds that at 20-25° C and 50-60% R.H., development was accelerated, so that a generation was produced in 1 year.

The differences between the accounts appears to be an egg diapause which has been observed in *Nemobius* populations in England and Czechoslovakia but not in France (or Germany?). On the available information it seems that the diapause, if it occurs, is facultative and the life cycle multi-voltine (Andrewartha 1952). That is, some of the eggs laid in any one year hatch almost immediately whilst the remainder over-winter and hatch the following, or in successive years. This interpretation would account for Chopard's observation of a July hatch, these eggs having undergone diapause, and also Rober's observation in October, the older nymphs having hatched in July (but been laid the year before) and the younger nymphs having hatched from eggs laid 3 months previously in July. Near the limits of its geographical distribution, in England and eastern Czechoslovakia, the facultative diapause results in a uni-voltine life cycle, so that normally all eggs undergo diapause and the generations are distinct.

The two generations present in the summer are not linked; a link only exists between alternate generations. Allee *et al.* (1949) speak of this phenomenon as annual cyclic isolation, a situation in which two genetically isolated populations exist together. The corollary is that there is no direct population density relationship between the coexistent generations. Cases of this type are supposedly of rare occurrence, and there are various means by which the isolation may be overcome. Some of the eggs may hatch either in the year in which they are laid or 2 or more years later, some of the nymphs may achieve maturity in their first summer without over-wintering, some of the nymphs may take more than one spring to complete their post-winter development, or some of the adults may over-winter and survive for a second breeding season. Work in the field and the laboratory suggests that none of these possibilities are of normal occurrence. In the first case the eggs would have to undergo diapause for more than one winter, but laboratory cultures show that this is not the case. The second and third possibilities cannot be supported by an examination of the samples. Nymphs do not mature in the first growing period, all nymphs undergo their sub-adult development in one spring, and adults die out at the end of the breeding season. *Nemobius*, therefore, appears to exhibit annual cyclic isolation in the sites under review.

(*a*) *Growth*

In each monthly collection one, two or more instars of *Nemobius* were present. Each instar, however, is a discrete entity recognizable on the basis of its head-width measurement (Gabbutt 1958). If one calculates the mean head-width of a generation for a particular monthly collection, it will be seen that this depends on the proportions of the different instars present. Over a period of time, changes in

this mean monthly head-width will reflect the growth taking place in the population.

Fig. 2 shows the mean monthly head-width for each generation plotted against time. There are two periods of growth. The gradual increase in the mean monthly head-width of the 1952 generation at Harpford 1 can be followed from July to November (Fig. 2). In November, growth is virtually at a standstill and the majority of the nymphs are fifth instars. Growth recommences in April and May, and that of the males and females can be followed until their maturity in August. This summary applies equally well to the generations at the other two sites (Fig. 2).

Richards (1949) showed that in some species of Orthoptera growth proceeds at a regular rate, and that the relationship between the linear measurement and time is unaffected by ordinary temperature fluctuations, provided each instar is subjected to the same mean temperature. A linear relationship exists between growth-

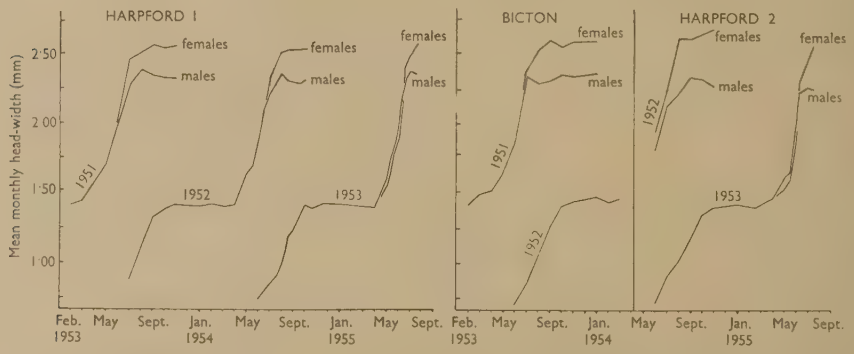

Fig. 2. The growth of the nymphs, males and females of the three generations shown at the three sites.

rate and time at certain periods during the life cycle of *Nemobius*. During the first growing period, mortality takes place, and it is possible that this may upset the proportions of the instars present. Mortality factors, however, appear to affect all instars equally, once they have reached the upper layers of the litter, because no unexpected discrepancies appear in the proportions of instars.

An approximation to the growth-rate has been calculated by fitting a linear regression to the mean monthly head-width data where the curve departs from the horizontal (Fig. 2). The P value for the regression coefficients is never higher than 0·05 and therefore is significant (Table 1).

At Harpford, observations extended over three seasons and it has been possible to compare the growth-rates of nymphs, males and females of the same or different generations (Table 2). Although no mathematically significant difference can be demonstrated between the growth-rates of males and females of the same generation (P always $> 0{\cdot}1$), the growth-rate of the females always tends to be greater. Growth commences in the sub-adult stages at approximately the same time in spring, and because the female is larger in mean head-width at maturity, the higher growth-rate diminishes the anticipated lag between the dates of male and

female maturation (Table 2). A comparison of the growth-rates for males and females of different generations shows that generally there is a significant difference from one year to the next. There is a significant difference between the

Table 1. *Growth-rates of* Nemobius

The general form of linear regression equation fitted to the data is $Y = mX+c$, where m is the regression coefficient describing the growth-rate, X is time, and Y is head-width. All regression coefficients are significant.

Generation		Equation	P for regression coefficient
HARPFORD 1			
1951	Male	$Y = 0{\cdot}0073X+1{\cdot}537$	$<0{\cdot}01$
	Female	$Y = 0{\cdot}0092X+1{\cdot}513$	$<0{\cdot}05>0{\cdot}02$
1952	Nymph	$Y = 0{\cdot}0080X+0{\cdot}887$	$<0{\cdot}05>0{\cdot}02$
	Male	$Y = 0{\cdot}0111X+1{\cdot}691$	$<0{\cdot}01$
	Female	$Y = 0{\cdot}0128X+1{\cdot}671$	$<0{\cdot}05>0{\cdot}02$
1953	Nymph	$Y = 0{\cdot}0050X+0{\cdot}702$	$<0{\cdot}01$
	Male	$Y = 0{\cdot}0124X+1{\cdot}655$	$<0{\cdot}01$
	Female	$Y = 0{\cdot}0144X+1{\cdot}482$	$<0{\cdot}01$
HARPFORD 2			
1954	Nymph	$Y = 0{\cdot}0050X+0{\cdot}718$	$<0{\cdot}01$
	Male	$Y = 0{\cdot}0097X+1{\cdot}402$	$<0{\cdot}01$
	Female	$Y = 0{\cdot}0117X+1{\cdot}311$	$<0{\cdot}01$
BICTON			
1952	Nymph	$Y = 0{\cdot}0063X+0{\cdot}674$	$<0{\cdot}01$

Table 2. *Comparisons of the significance of the difference between the growth-rates at Harpford 1 of* (a) *males and females of the same generation,* (b) *males and females of different generations,* (c) *nymphs of different generations*

	Generations		P
(a)	1951	Males+Females	$>0{\cdot}10$
	1952	Males+Females	$>0{\cdot}10$
	1953	Males+Females	$>0{\cdot}10$
(b)	1951+1952	Males	$<0{\cdot}05>0{\cdot}02$*
	1952+1953	Males	$>0{\cdot}10$
	1951+1953	Males	$<0{\cdot}01$*
	1951+1952	Females	$>0{\cdot}10$
	1952+1953	Females	$<0{\cdot}05>0{\cdot}02$*
	1951+1953	Females	$<0{\cdot}02>0{\cdot}01$*
(c)	1952+1953	Nymphs	$<0{\cdot}02>0{\cdot}01$*

* Significant.

growth-rates of the nymphs of the 1952 and 1953 generations (P is between 0·01 and 0·02).

It might be supposed that, because *Nemobius* reaches the limit of its northern distribution in England, temperature is likely to be a limiting factor. Any analysis is speculative because there is insufficient data from microclimatological studies to

estimate the full effect of insolation, and metereological information is not accurate enough for this purpose. Suffice it to record that no connection was found between growth-rate and the gross metereological figures for temperature and rainfall in this area. It is suggested that the insulation provided by the litter and its actual physical structure tend to mitigate climatic effects, and the complexity of these relationships can only be adequately assessed by a thorough study of the microclimate in the litter.

It has been shown that the coefficient of a linear regression is a measure of the growth-rate during two periods of the life cycle. Mean monthly head-width was plotted against time. If the known head-width of each instar is successively substituted in the regressions then values for the other variate, time, will be approximations of the time spent in each stage.

If only one instar is present in a monthly collection, the mean monthly head-width of the generation coincides with the mean head-width of the instar. If the regression is extrapolated to the point where the line coincides with the mean

Table 3. *The length (days) of the nymphal stages*

A, estimated date when only the first instar was present; *B*, estimated earliest theoretical date of hatching.

Generation		Stages					Total	*A*	*B*
		1	2	3	4	5			
Harpford 1	1952	19·2	18·3	23·8	21·6	22·5	105·4	11 July	22 June
	1953	31·1	32·4	35·8	37·7	38·4	175·4	1 July	1 June
Harpford 2	1953	41·6	34·2	32·9	42·3	–	–	9 June	9 May
Bicton	1952	23·7	31·6	23·1	31·1	–	–	5 July	11 June

head-width of the first instar, this represents a time, *A*, during the period of hatch when only first instars were present. If the time spent in the first stage is subtracted from time *A*, the difference gives an estimate of the earliest theoretical date of hatching, time *B*. The actual period of hatch cannot be determined, but the date on which it commenced must have been between *A* and *B*. If this were not so, second instars would be present at time *A* and the mean monthly head-width could not have coincided with the mean head-width of the first instar. These estimates are difficult to check in the field, but it is suggested that they are good approximations.

Consider the 408 and 406 nymphs collected at Harpford 1 in August and September 1953. The time interval between the two collections was 30 days. Mortality appeared to be balanced by hatching so that the net result was a population stable in numbers. Two assumptions are made: that the time spent in each stage was 20 days (compare 18·3, 23·8, 21·6 and 22·5 days spent as first, second, third and fourth instars (Table 3)), and that the age of the individuals was 1, 2, 3, ... days old up to the next stage minus 1 day. In the case of the forty-seven second instars present in the August collection 20/30 (two-thirds) will be third instars and 10/30 (one-third) will be fourth instars in September. Applying

these proportions to all the observed August figures and bearing in mind that *Nemobius* over-winters as the fifth instar, then the theoretical distribution of numbers per instar can be compared to the observed figures (Table 4). The difference between the September observed and calculated figures can be accounted for by chance alone ($P > 0{\cdot}7$). The initial assumption of 20 days gives results,

Table 4. *The observed and calculated numbers of nymphs at Harpford 1 (1953)*

	Instars					Total
	2	3	4	5	6	
August (observed)	47	235	126	–	–	408
September (calculated)	–	31	16			
	–	–	157	77	–	
	–	–	–	84	42	
Total		31	173	203		407
September (observed)	–	28	179	199		406

therefore, which indicate that the stage lengths calculated from the regressions are reasonably correct.

The substitution of the mean head-width of the fifth instar in the regressions for males and females gives the approximate date on which growth commenced in the population in spring. This is not very reliable because it is affected by the rate at which the population attains the mean growth-rate, and not all the over-wintering nymphs are fifth instar. The calculated end point of this growing period is much more precise and is obtained by substituting the mean head-width of adults in the

Table 5. *Length (days) of the male and female stages with estimated length of the period of growth*

Generation		Stages				Total	Growing period	
		5	6	7	8		Start	Finish
MALES								
Harpford 1	1951	25·1	20·1	39·7	38·4	123·3	4 April	6 August
	1952	16·2	14·4	29·3	18·6	78·5	11 May	29 July
	1953	15·1	12·9	24·5	19·7	74·1	8 May	20 July
Harpford 2	1953	17·8	17·9	34·5	14·4	84·6	29 April	23 July
FEMALES								
Harpford 1	1951	19·9	23·9	31·5	45·0	120·3	12 April	10 August
	1952	14·1	23·8	24·2	22·8	84·9	16 May	9 August
	1953	12·5	17·3	25·4	24·5	79·7	17 May	5 August
Harpford 2	1953	16·6	21·3	33·9	23·1	94·9	7 May	10 August

male and female regressions. The total length of this growing period is approximately the same for both males and females. There is, however, a lag of about 10 days because the females commence growth a little later in the spring (5-9 days, Table 5). The higher mean head-width of the female is balanced by the consistently but not significantly higher growth-rate.

(b) The period of hatch

The over-wintering eggs hatch the following spring and the period of hatch is important with respect to mortality and the 'staggering' of the instars over the remainder of the summer. In different cultures in the laboratory the date on which hatching commenced varied from 5 May to 20 June (46 days) and ceased on 7 July to 10 September (65 days). The average total length of the period was 70 days with a range of 52 to 98 days. It appears unlikely that these figures are as high in the field. Hatching over such a period would result in first instars being present in the field collections for 70 days plus the length of the first stage. This is not the case, as first instars were present only for 30-50 days.

It is not possible to estimate very accurately the length of the hatching period from the field data, but minimum and maximum periods can be determined by considering the time of appearance of the first instar. In the case of collections at Harpford 1 (Fig. 1) first instars of the 1953 generation were collected over 42 days on 20 June, 9 July, 20 July and 1 August, but were not present in the collections of 3 June or 24 August (*i.e.* over 81 days). The maximum period of hatching can be calculated if we assume that the eggs started hatching immediately after the

Table 6. *Length of hatching period (days)*

	Harpford 1		Harpford 2	Bicton
Generation	1952	1953	1953	1952
Minimum	6	11	–	10
Maximum	40	50	–	68
More probable minimum	15	30	33	21
More probable maximum	40	53	65	46
Averages	27·5	41·5	49	33·5

collection on 3 June and they were all second instars just before the collection on 24 August. This period minus the length of the first stage represents the maximum period; *i.e.* 81—31 = 50 days. If the eggs started hatching just before the collection on 20 June and only second instars were present on 1 August, then this period minus the length of the first stage gives the minimum hatching period; *i.e.* 42—31 = 11 days. The earliest possible date of hatching was 1 June (*B*, Table 3) and although no first instars were collected on 3 June, it is probable that they were not present at a sufficiently high density to be detected by the sampling method. If the second instars collected on 9 July had only just entered that stage then they must have hatched on 8 June (9 July minus 31 days). This suggests that the hatch was nearer to 1 June than 20 June and that the calculated earliest date of hatching is a reasonable approximation. Using this calculated date (Table 3) then a more probable range is 30-53 days (*i.e.* 1 June to 1 August minus 31 days = 30 days and 1 June to 24 August minus 31 days = 53 days). The mean period is 41·5 days and this is compatible with the presence and absence of first and second instars in the field collections. Using similar arguments the results are shown in Table 6 for the other sites.

(c) Fecundity

A direct measure of fecundity was found to be impracticable in the field, since the eggs are laid singly in the rich organic matter of the litter or the soil, and this makes their separation difficult by a flotation technique and hand sorting is laborious. Measurements had therefore to be indirect.

An examination of gravid females from the collections at Harpford 1 in 1953 and 1954 showed that many eggs were present in the panoistic ovarioles but 'ripe' eggs were those which were present in the oviduct, possessed hard cuticular coats and were greater than 1·60 mm in length. The number of such ripe eggs increases from July until a peak is reached later in the year; in October 1953 and in September 1954. These peaks are significant when compared to the lowest mean number of eggs present in July 1953 and 1954 ($P < 0{\cdot}01$). If the number of ripe eggs is indicative of the rate of laying, then this increases later in the season. Two other points are relevant, that the laying period appears to extend over the whole of the female's adult life, and that the rate of laying decreases towards the end of the summer.

One male and one female were kept in a Brefitt jar at room temperature. Twenty-one such jars were used over the period July 1953 to October 1954. Each was provided with a layer of sterilized sand for oviposition. Initially the females were virgin, that is they were collected as immatures in the field and separated from the males until their final moult. Observations show that the female starts ovipositing 7-12 days after this moult so that 10 days have been subtracted from the total length of the adult stage to give the time during which the female was normally expected to lay eggs. At the end of the breeding season, when the females died, the eggs were removed from the sand by flotation, sand being mixed with a solution of magnesium sulphate of sp. gr. 1·2 and compressed air forced through the suspension to facilitate mixing. The eggs which floated to the surface were washed in water. Careful hand sorting of the sand after the operation showed that the method was nearly 100% efficient as only six additional eggs were discovered out of a total of 2189. The washed eggs were kept in sterilized sand in covered Petri dishes and left at $16 \pm 2°$ C over the winter. When hatching took place the following spring the percentage hatch was calculated (Table 7). The mean number of days on which the female was potentially able to lay eggs was approximately 66 ± 21 days and the females laid $1{\cdot}56 \pm 0{\cdot}54$ eggs per day during this time; 39% of these eggs hatched. Six perforated zinc cages each containing five males and five females were set out in the field at Harpford 1. The cages were visited normally every 5 days to establish the longevity of the females. The eggs, which were laid in sand, were extracted by the flotation technique and kept in the laboratory at $16 \pm 2°$ C (Table 8). Females were available to lay eggs on 70 ± 18 days (76 ± 10 days), and produced 0·94 eggs per day of which 58·2% hatched. If the anomalous data from cage C are omitted (Table 8), the figures become 1·00 egg/day and 59·8% hatch. The percentage hatch is remarkably low, and may be accounted for wholly or partly by failure to hatch attributable to the magnesium sulphate technique, a genuine sterility, possibly due to a complex mating behaviour

Table 7. *Data from the laboratory cages (1953-4)*

Figures show the total number of eggs laid by each female, the total hatch, the percentage hatch, the number of days on which a female was normally expected to lay (longevity – 10 days) and the average number of eggs laid per day.

Cage	Total eggs laid	Total hatch	Hatch (%)	Number of days on which female normally expected to lay eggs	Average number of eggs per day
A	137	54	39·4	47	2·91
B	67	47	70·1	41	1·63
C	114	26	22·8	90	1·27
D	97	27	27·8	78	1·24
E	100	26	26·0	90	1·11
F	191	64	33·5	90	2·12
G	139	73	52·5	69	2·01
H	108	5	6·0	90	1·20
K	142	89	62·6	90	1·58
L	152	101	66·4	73	2·18
M	69	39	56·5	64	1·08
N	68	1	–	43	1·58
P	51	31	60·8	36	1·42
Q	108	41	38·0	76	1·42
R	43	5	11·6	58	0·74
S	128	62	48·4	64	2·00
T	220	133	60·4	82	2·68
U	93	28	30·1	72	1·29
V	53	2	–	59	0·90
X	93	–	–	65	1·43
Z	16	–	–	12	1·33
Totals	2189	854			
Means and averages			39·0	66·14	1·56
Standard deviation				±20·62	±0·54

Table 8. *Data from field cages kept at Harpford 1 (August-October 1954)*

Each cage contained five males and five females.

Cage	Total eggs laid	Total hatch	Hatch (%)	Number of days on which females normally expected to lay eggs*	Average eggs/day/female
A	302	178	58·9	375	0·81
B	398	201	50·5	405	0·98
C	71	11	15·5	185	0·38
D	427	239	56·0	385	1·11
E	451	307	68·1	395	1·14
F	337	221	65·6	345	0·98
Total	1986	1157			
Total minus cage C	1915	1146			
Means and averages			58·2	69·7 ± 17·80	0·94 ± 0·08
Means and averages minus cage C			59·8	76·2 ± 9·93	1·00 ± 0·04

* To the nearest 5 days.

(Gabbutt 1954), or the condition of the sand (soil wetness and structure) at the time of hatching.

In relation to the third alternative, observations in the laboratory show that when the eggs hatch, the 'vermiform larvae' reach the surface by means of undulatory movements. The typical first instar is assumed when the 'larva' casts its skin. It is suggested that the persistence of the 'vermiform larva' is determined by contact or pressure factors. The 'larva' moults when it is freed from contact with soil particles, that is when it reaches the surface or enters a soil cavity. In the latter case, the resulting nymph is trapped and eventually dies and thus the soil structure may be an important limiting factor during the hatching period. The surface tension of a single drop of water is sufficient to hold and eventually kill the delicate first instar immediately after the 'vermiform larva' has moulted. It is possible to account for the discrepancy in hatching success in the cultures in terms of soil wetness and an experiment was conducted to verify this conclusion.

Two sets of two Petri dishes were used. One hundred eggs were placed in each dish. These were obtained by hand sorting to eliminate any detrimental effect from the flotation technique. Both sets of eggs were kept at $16 \pm 2°$ C over the

Table 9. *Hatching success (%) for two sets of laboratory cultures*

Dish	Continually watered	Watering stopped 23 days before hatching
A	42	–
B	50	–
Average	46	–
C	–	69
D	–	84
Average	–	76·5

winter. Dishes A and B were saturated with water every 3 days up to the date of hatching while dishes C and D were only watered until 23 days before hatching commenced. The results (Table 9) suggest that the amount of water in the soil can play a decisive role at the time of hatching, and this together with the structure of the soil may be the cause of the high mortality taking place during this period. The unexplained failure to hatch amounts to between 16 and 31% of the total, and this may be due to infertility factors or deterioration during the winter. No egg parasites were found.

(*d*) *Sex ratio*

In 1953, 1954 and 1955 the density of males and females at Harpford 1 for each generation agrees well with a 1 : 1 ratio. Generally speaking, any departures from this ratio can be accounted for by chance alone (P high and not significant). Although there were significant departures, an interaction chi-square for each year's collection shows no significant heterogeneity between the samples. Such discrepancies represent local sampling errors. The sex ratio at Harpford 2 approximates to a 1 : 1 ratio, the samples again appearing homogeneous. At Bicton in

1953, there were significant departures from the assumed 1 : 1 ratio and an interaction chi-square indicates that the samples were markedly heterogeneous. The average density of the males and females over the breeding season is shown in Table 10.

Table 10. *Average density per square metre over the breeding season*

Generation		Males	Females
Harpford 1	1951	11·40	11·08
	1952	7·72	9·28
	1953	8·84	10·24
Harpford 2	1952	4·20	3·73
	1953	4·66	4·62
Bicton	1951	4·13	10·24

(*e*) *Mortality*

During the summer, mortality factors act independently on the two generations present. Very little mortality takes place in the adult stage but mortality factors act overwhelmingly on the first five instars during the summer following the hatch. The level to which this nymphal population falls, approximates to that at which it will exist as adults the following year. It is not possible to estimate the mortality rate over the hatching season because the rate at which young nymphs enter the population (the birth rate) is not known. An estimate of the mortality rate has been made, therefore, after the peak population has been reached. A regression of the form $\log_e Y = mX + c$ (see Table 11) has been used and there is good correla-

Table 11. *Mortality rates*

Regression equations fitted to the nymphal data have the general form: $\log_e Y = mX + c$, where m is the regression coefficient representing the mortality rate, X is time, and Y the number of nymphs surviving at the time of collection. All the regression coefficients are significant.

Generation		Equation	P (for regression coefficient)
Harpford 1	1952	$\log_e Y = 5{\cdot}994 - 0{\cdot}0230X$	$<0{\cdot}05>0{\cdot}02$
	1953	$\log_e Y = 6{\cdot}172 - 0{\cdot}0300X$	$<0{\cdot}01$
Harpford 2	1953	$\log_e Y = 4{\cdot}182 - 0{\cdot}0108X$	$<0{\cdot}05>0{\cdot}02$
Bicton	1952	$\log_e Y = 5{\cdot}478 - 0{\cdot}0140X$	$<0{\cdot}01$

tion between the data and the fitted line (P values for the regression coefficient never $> 0{\cdot}05$). The fitting of the data to a regression of this form suggests that mortality is dependent on density, so that the mortality rate drops as the numbers fall off. The rate was different at the three sites but at each it was associated with different initial densities. It is possible, using the regressions for the data from Harpford 1 in 1954 to calculate three extrapolations, if it is assumed that the mortality rate is of the type indicated by the regressions and operates over the hatching period, and that the length of the period of hatch is 42 days (Table 6).

By substituting the calculated earliest date of hatching (Table 3) the number of nymphs which must have been present on certain dates to satisfy the mortality rates can be calculated. It is probable that the rate of hatching follows a normal distribution so that the figure calculated for the middle of the period is presumably correct. The results of this substitution are shown in Table 12.

The number of eggs of the 1953 generation which are laid by the adult population at Harpford 1 depends on three factors, the period over which the females lay

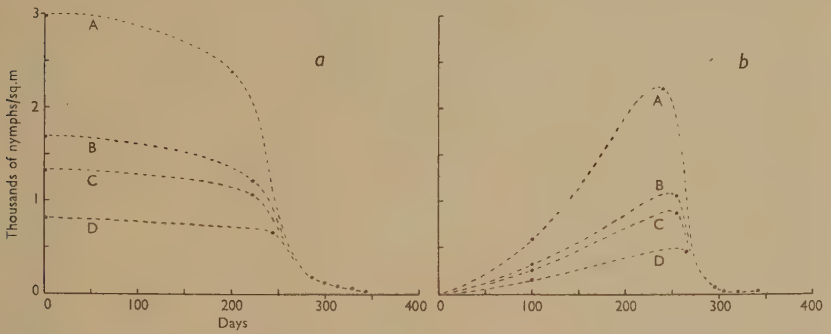

Fig. 3. Four estimates, A, B, C and D (based on Table 13—see text) for the 1953 generation of *Nemobius sylvestris* at Harpford 1 in 1954 of: *a*, the survivorship curve showing the density of nymphs alive after certain time intervals; *b*, the death curve showing the density of nymphs dead after certain time intervals.

eggs (about 120 days—Fig. 1), the average density of the females (11/sq. m—Table 10), and the rate at which each female lays (1 egg/day—Table 8). The number of eggs laid, therefore, is $120 \times 11 \times 1 = 1320$/sq. m. Assuming, on the basis of the experimental work, that 20% of the eggs are infertile or do not hatch, then the eventual nymph density will be 1056/sq. m. This estimate agrees reasonably well with the 1230/sq. m (Table 12) calculated half-way through the hatching period from the extrapolated mortality data. The lowest calculated figure of 640/sq. m lies well within the reproductive capacity of the female, and the highest

Table 12. *The density per sq. m of nymphs present at Harpford 1 on certain dates to satisfy the mortality rates*

1 June 1954 earliest date of hatching – 0 days	22 June 1954 middle of hatching period – 21 days	13 July 1954 latest date of hatching – 42 days
2390	1230	640

figure of 2390/sq. m demands a rate of laying of the order of 2·5 eggs/day, which has been achieved in the laboratory.

The distribution of mortality in the 1953 generation at Harpford 1 (1954) can be calculated. The survivorship curve (Fig. 3) plotted from the data in Table 13 shows the density of this generation at the end of particular time periods. The death curve (Fig. 3) plotted from the results in Table 13 shows the fall in density

during particular time intervals; the figures being related to the mid-point of the period. Four estimates are plotted for each curve, three (A, B, D) being derived from the extrapolated mortality data (Table 12) and C from the fecundity data. The initial number of eggs available is in the region of 1320-1530/sq. m and the percentage mortality from these two estimates (B, mortality and C, fecundity data) indicates the more probable trend, whilst the two further estimates, A and D, indicate the possible range in percentage mortality. The mortality can be con-

Table 13. *Survival and mortality of the 1953 generation at Harpford 1*

Four possible estimates (A, B, C and D - see text) of the numbers (% in parentheses) of eggs and nymphal stages per sq. m surviving and dying during the stated time intervals. The time elapsed since laying ceased the year before was approximately 200 days.

1954	Days elapsed		Estimates (see text) A	B	C	D
Initial no. of eggs	0		2988	1358	1320	800
EGGS SURVIVING (80% of those laid)						
1 June	200		2390	–	–	–
22 June	222		–	1230	1056	–
13 July	244		–	–	–	640
NYMPHS SURVIVING		No./sq. m	%			
24 August	286	184·8	6·18	12·02	14·00	23·10
5 September	298	123·6	4·14	8·04	9·36	15·45
20 September	313	92·0	3·08	5·98	6·97	11·50
5 October	328	67·6	2·26	4·40	5·12	8·45
20 October	343	28·8	0·96	1·87	2·18	3·60
EGGS DEAD			eggs/sq. m (%)			
1 June	200		598 (20)	308 (20)	264 (20)	160 (20)
	243		2205 (73·8)	–	–	–
	254		–	1055 (68·0)	871 (66·0)	–
	265		–	–	–	456 (56·9)
NYMPHS DEAD		No./sq. m	%			
	292	61·2	2·04	3·98	4·64	7·65
	305	31·0	1·06	2·06	2·39	3·95
	320	24·4	0·82	1·58	1·85	3·05
	343	38·8	1·30	2·53	2·94	4·85
20 October	343	total dead	99·04	98·13	97·82	96·4

sidered as taking place in four stages: 20% (16-31%) in the egg stage—this estimated figure is based on laboratory work and is attributed to an infertility factor or deterioration of the eggs over the winter—67% (57-74%) over the period of hatch—probably soil wetness and soil texture cause mortality before the 'vermiform larva' reaches the surface of the soil, and the free water in the lower layers of the litter may also be detrimental to the first instar; once this instar reaches the upper and drier litter layers predators may cause losses in the population—11% (5-20%)

over the remainder of the first growing period affecting all instars up to and including the sixth and attributable to predation, and 2% (1-3%) in the second growing period and among adults.

FOOD AND FEEDING HABITS

Several workers have contributed to our knowledge of the food and feeding habits of this insect (Turk 1858, Lucas 1916, 1920, Syms 1938, Rober 1949, Touratier 1951, Richards 1952). Their work is summarized in Table 14; most of the observations were made on insects in captivity but field observations are noted. The author has seen *Nemobius* in the field feeding on honeysuckle leaves, oak leaves

Table 14. *The food accepted* (+) *and refused* (0) *according to various authors*

	Turk (1858)	Lucas (1916, 1920)	Syms (1938)	Rober (1949)	Touratier (1951)	Richards (1952)
Honeysuckle leaves	–	–	–	–		+
Oak leaves	–	–	–	–	+	–
Poplar leaves	–	–	–	–	+	–
Elm leaves	–	–	–	–	+	–
Walnut leaves	–	–	–	–	+	
Burnet leaves	–	–	–	–	+	–
Eglantine leaves	–	–	–	–	+	–
Hornbeam leaves	–	–	–	–	0	–
Beech leaves	–	–	–	–	0	–
Rose leaves	–	0			–	–
Nasturtium leaves	–	0	–	–		–
Service leaves	–	+	–	–		–
Fungi	–	+[1*]	–	–	–	+[2]
Leaf galls	–	–	–	–	–	+[3]
Acorns	–	–	–	–		+
Apple	–	–	–	+	–	+*
Dead insects	+	–	+	+	–	+[4]
Vegetable matter	–	–	+	–	–	–
Grasses	–	–	–	–	–	–
Insect larvae	+	–	–	–	–	–

[1] *Boletus* sp.
[2] *Clavaria* sp., *Cantharellus cibarius*, *Psalliota campestris*, *Boletus* sp., *Phallus impudicans*.
[3] *Neuroterus lenticularis* and *N. numismatis*.
[4] Diptera, Aphididae and Cercopidae.
* Field observations.

and the succulent parts of *Luzula*. Only 'natural' foods appear in Table 14 but others worthy of mention are bread, raw meat, cork, banana (Lucas 1920), raw potato (Syms 1938), lettuce, runner bean, cheese, nuts (chestnut, peanut and coconut) (Richards 1952). Potentially, therefore, *Nemobius* is omnivorous in its feeding habits. Opinions as to the main food source are conflicting. Turk (1858) suggests that insect larvae and dead insects are taken in preference to vegetable matter, whilst Richard (1952) believes that the smaller moulds and mildews present on the decaying oak leaves are important in the diet.

The gut contents were examined by making a mid-dorsal incision in the body wall and removing the alimentary tract intact by cutting through the oesophagus and hind gut. As the contents of the posterior gut are unrecognizable, only the

contents of the crop and gizzard were smeared on a slide. Forty-nine specimens were examined, of which twenty-nine were adults and the remaining twenty were fifth instar. This material indicates that most of the food at the sites is of vegetable origin. All specimens examined had angiosperm remains judging from the nature of the material which was mostly phyllaceous. Oak leaves were present in forty-two cases, these being recognized by the fine stellate hairs on the leaf surface. Fungal hyphae appeared in profusion in all but three cases and fat globules and starch grains were present in all specimens. In three of these the starch grains appeared to be very similar to those produced in suspension when an acorn was crushed in a little water. Occasional moss remains were found. Animal material was noted in only one specimen and it is possible that this was exuvial because the nymph appeared to have moulted recently. No difference could be detected between the stomach contents of the nymphs and adults.

Touratier (1951) showed that the nymphs have a distinct preference for dry leaves rather than green leaves of the same species. Table 14 shows the leaves most generally accepted and it is interesting to note that beech leaves were generally refused; dry oak leaves were particularly favoured. Observations in the field confirm a preference for oak leaves, and show no particular discrimination between the upper and lower surfaces, and that the destruction of the leaves is neither as total nor as systematic as that described by Touratier. In the laboratory where a large number of nymphs are provided with a small number of leaves, the rate at which the leaves are destroyed might be expected to depend on the density of the animals and the palatibility of the leaf parts. In the field the density of the nymphs, at least in England, is comparatively low in relation to the leaves available so that the systematic and destructive effect is not apparent. The leaves only suffer superficial damage, the ground tissue usually being eaten away in only a few small and isolated areas. There is no tendency for the nymphs to congregate together and systematically destroy the leaves so that the phenomenon reported by Touratier can probably be accounted for on the basis of the unnaturally high density of nymphs in his experiments. He does show, however, that virtually all parts of the oak leaves can be eaten by *Nemobius* so that, as damage to the leaves is slight in the field, the insect is probably living well within the capacity of its food supply.

PREDATORS

It is notoriously difficult to collect information on predator–prey relationships especially in the case of a cryptozoic fauna. A quantitative estimate has been made of the density of various predators in the field and the importance of these is assessed with reference to actual observations in the field and laboratory. Observations on predators which have been seen to take *Nemobius* in the field are summarized in Table 15. The paucity of these records emphasizes the difficulties in accumulating information of this sort.

The design of the experiments in the laboratory depended upon the availability both of the nymphal stages of *Nemobius* and the predators concerned. Although adult lycosid spiders were not present in the monthly collections after June they

were kept alive in the laboratory until September and took most of the instars offered. The adults when attacked by these spiders were able to kick them away using their hind legs. The lithobiids, pseudoscorpions and Coleoptera normally took only the first five instars, the later instars appearing to be too big for these

Table 15. *Predators observed eating* Nemobius sylvestris *in the field*

	Nemobius instars		*Nemobius* instars
Lycosa sp. sub-adult	5♂	*Geophilus carpophagus* juv.	3
Lycosa sp. juvenile	2, 4	*Lithobius duboscqui*	3
L. amentata	7♂	*L. duboscqui* juvenile	4
Pisaura mirabilis	5♀	*Notiophilus rufipes*	2
Salticus scenicus	5♀	*Neobisium muscorum*	1
Trochosa sp. juvenile	7♀		

predators to capture. The results of the feeding experiments in the laboratory are summarized in Table 16.

Predators were collected in the field (see p. 16) at Harpford 1 from February 1953 to May 1954 and at Harpford 2 from June 1954 to May 1955. At each site twenty-five samples, each of area 0·1 sq. m were removed from a total sample area of 250 sq. m, the sites normally being visited once a month. The leaf litter was

Table 16. *The instars of* Nemobius sylvestris *which have been taken* (−) *or refused* (0) *by named predators in the laboratory*

	Instars												
	1	2	3	4	5	6		7		8		Adults	
						♂	♀	♂	♀	♂	♀		
Lycosa lugubris	−	+	+	+	−	−	−	0	0	0	+	0	0
L. amentata	+	+	+	+	−	−	−	−	−	−	−	0	0
Pisaura mirabilis	−	−	−	−	−	+	−	−	+	+	+	0	0
Lithobius duboscqui	+	+	+	+	+	−	−	−	−	−	−	0	0
L. forficatus	−	+	−	+	−	−	−	0	0	0	0	0	0
Notiophilus rufipes	+	+	+	+	−	−	−	−	0	−	0	0	0
Lithobius calcaratus	+	+	+	+	−	−	−	−	−	−	−	−	−
Chthonius ischnocheles	+	+	+	+	+	−	−	−	0	−	0	0	0
Neobisium muscorum	+	+	+	+	−	−	−	−	−	-	-	−	−

removed from the quadrat by hand and transferred to tins. Any predatory species encountered during this operation were collected separately and preserved in 70% alcohol. Only the 'F' layer and that part of the 'H' layer which still had recognizable leaf fragments were removed (Hessleman 1926). Great care was taken not to break into the 'A' or mineral soil layer. Once the quadrat had been cleared the tins were sealed. In the laboratory the samples were transferred to the trays of the Tullgren apparatus, and again any animals encountered were collected and preserved separately.

The Tullgren funnels were of conventional design and consisted of three parts: a funnel, a tray incorporating a sieve, and a cover. The funnel was cone shaped and received at its lower end a tube containing 70% alcohol and 5% glycerine. All

parts were made of highly polished aluminium except the sieve, which was of copper wire gauze 7 mesh 20 S.W.G. (mesh width 5 mm). The tray had a diameter of 41 cm and 8 cm sides. The cover fitted tightly over the tray into the recessed edge of the funnel. The top of the cover had a small hole from which a 40 W electric light bulb was suspended 20 cm above the surface of the litter when the apparatus was in use. Six such funnels were used and each sample spent between 2·5 and 4 days in the apparatus, depending on water content. As twenty-five samples were taken each month, shortage of funnels resulted in some of the samples remaining sealed in their tins for as long as 12 days. The losses which occurred during this time remain an unknown source of error. They were assumed to be small because there was a plentiful supply of prey animals available in the litter to forestall death by starvation. Moreover, most of the predators considered here (*e.g.* spiders) can exist for long periods without food. After extraction, the predators were examined in a

Table 17. *The efficiency of the Tullgren funnel with respect to named species*

		Experiments			Total
		1	2	3	
Lycosa sp. juveniles	Introduced	11	12	15	38
	Recovered	8	9	11	28
	Recovery (%)	73	75	74	74
Linyphiid spp. juveniles	Introduced	23	31	19	73
	Recovered	10	20	13	43
	Recovery (%)	44	65	68	59
Geophilus carpophagus (various stages)	Introduced	19	29	6	54
	Recovered	18	26	2	46
	Recovery (%)	95	90	33	65
Lithobius duboscqui (various stages)	Introduced	36	22	31	89
	Recovered	32	21	25	78
	Recovery (%)	89	95	81	88
Notiophilus rufipes	Introduced	11	7	3	21
	Recovered	9	5	3	17
	Recovery (%)	82	71	100	81
Chthonius ischnocheles (various stages)	Introduced	16	9	11	36
	Recovered	16	5	7	28
	Recovery (%)	100	56	64	78

Petri dish under a binocular microscope at ×20. The dish was searched systematically against a background of white cardboard engraved with black lines until two successive examinations yielded no additional predators. The amount of litter which fell through the sieve was neglible and did not hinder the examination.

A rough estimate of the efficiency of the Tullgren funnels was made following Van der Drift's method (1951). Sterile litter was used and after wetting, a known number of animals were introduced. The light was switched on and the number of animals appearing in the collecting tubes were noted. The experiment was allowed to run for 3 days, by which time the litter had been thoroughly desiccated. The percentage recovery was calculated and the results are shown in Table 17. Efficiency varies between 59% and 88% for the groups considered. A list of predatory species is given in Table 18 and the following notes on the more important groups amplify this information.

Table 18. *Predatory species associated with* Nemobius sylvestris *at Harpford 1 and Harpford 2*

COLEOPTERA
Carabidae
Notiophilus rufipes Curtis
N. biguttatus (Fabr.)
Badister bipustulatus (Fabr.)
Ophonus sp.
Bradycellus verbasci (Duftschmid)
Amara plebeja (Gyllenhal)
A. tibialis (Paykull)
Feronia madida (Fabr.)
Abax parallelopipedus (Piller & Mitterpacher)
Calathus piceus (Marsham)
Metabletus truncatellus (L.)
M. foveatus (Fourcroy)

Silphidae
Leptinus testaceus Mueller
Nargus wilkini (Spence)

Clambidae
Stenichus collaris (Mueller & Kunze)

Staphylinidae
Proteinus brachypterus (Fabr.)
Astenus gracilis (Paykull)
Lathrobium brunnipes (Fabr.)
Leptacinus bathychrus (Gyllenhal)
Xantholinus longiventris Heer
Gauropterus fulgidus (Fabr.)
Gyrohypnus punctulatus (Goeze)
G. augustus (Stephens)
G. myrmecophilus (Kiesenwetter)
Philonthus laminatus (Creutzer)
P. addendus Sharp
P. fuscipennis (Mannerheim)
P. longicornis Stephens
Quedius fumatus Stephens
Q. picipes (Mannerheim)
Q. boops (Gravenhorst)
Habrocerus capillaricornis (Gravenhorst)
Tachyporus tersus Erichson
T. chrysomelinus (L.)
T. solutus Erichson
Amischa analis (Gravenhorst)
Alaobia scapularis (Sahlberg)
Atheta trinota (Kraatz)
Aleochara cuniculorum Kraatz
Acronota fungi (Gravenhorst)

Coccinellidae
Adalia decempunctata (L.)

ARANEIDA
Ciniflo fenestralis (Stroem)
C. similis Blackwall
Dysdera crocota C. L. Koch
Drassodes lapidosus (Walckenaer)
D. pubescens (Thorell)
D. signifer C. L. Koch
Drassodes sp. juvs.
Zelotes latreilli (Simon)
Micaria pulicaria (Sundevall)
Clubiona sp. juvs.
C. compta C. L. Koch
C. pallidula (Clerck)
C. terrestris Westring
Zora spinimana (Sundevall)
Phrurolithus festivus C. L. Koch
Oxyptila sp. juvs.
O. trux (Blackwall)
Xysticus cristatus (Clerck)
X. kochi Thorell
Salticus scenicus (Clerck)
Heliophanus cupreus (Walckenaer)
Evarcha falcata (Clerck)
Hypomma cornutum Bosenberg
Micrargus herbigradus (Blackwall)
Lycosa sp. juvs
Lycosa lugubris (Walckenaer)
L. amentata (Clerck)
Trochosa terricola Thorell
Pisaura mirabilis (Clerck)
Agelena labyrinthica (Clerck)
Amaurobius terrestris (Wider)
A. atropos (Walckenaer)
Pholcomma gibbum (Westring)
Robertus lividus (Blackwall)
Meta segmentata (Clerck)
Araneus diadematus (Clerck)
Ceratinella brevis (Wider)
C. scabrosa (O. P. Cambridge)
Wideria antica (Wider)
Walckenaera acuminata Blackwall
Maso sundevalli (Westring)
Monocephalus fuscipes (Blackwall)
Savignia frontata (Blackwall)
Microneta viaria (Blackwall)
Lophocarenum parallelum (Wider)
Diplocephalus cristatus (Blackwall)
D. latifrons (O. P. Cambridge)
D. picinus (Blackwall)
Meioneta rurestris (C. L. Koch)
Centromerita bicolor (Blackwall)
C. concinna (Thorell)
Centromerus dilutus (O. P. Cambridge)
C. sylvaticus (Blackwall)
Tapinopa longidens (Wider)
Oreonetides abnormis (Blackwall)
Macrargus rufus (Wider)
Leptyphantes tenuis (Blackwall)
L. zimmermanni Bertkau
L. flavipes (Blackwall)
L. mengei Kulczynski
Linyphia triangularis (Clerck)
Bathyphantes concolor (Wider)

CHILOPODA
Haplophilus subterraneus (Leach)
Schendyla nemorensis (C. Koch)
Chaetechlyne vesuviana (Newport)

Scolioplanes crassipes (C. Koch)
S. acuminatus (Leach)
Necrophloephagus longicornis (Leach)
Geophilus carpophagus (Leach)
Brachygeophilus truncorum (Bergsö & Meinert)
Cryptops hortensis Leach
Lithobius variegatus Leach
L. forficatus (L.)
L. calcaratus C. Koch
L. duboscqui Brolemann

Pseudoscorpiones
Chthonius ischnocheles (Hermann)
Neobisium muscorum (Leach)
Microcreagris cambridgei (L. Koch)
Roncus lubricus L. Koch

Thirty-five species of Coleoptera were taken at Harpford 1 and twenty at Harpford 2, fourteen being common to both sites. The seasonal variations for the total density are shown in Fig. 4. The two most important species were *Notiophilus rufipes* and *Gyrohypnus myrmecophilus* although their density was low. Both species were more abundant as adults, reaching a maximum density of 33·6 and 35·6 per sq. m at Harpford 1 and 2 respectively.

The spiders from the two sites have been described in detail by Gabbutt (1956). Forty-nine species were recovered from the litter at Harpford 1, thirty from

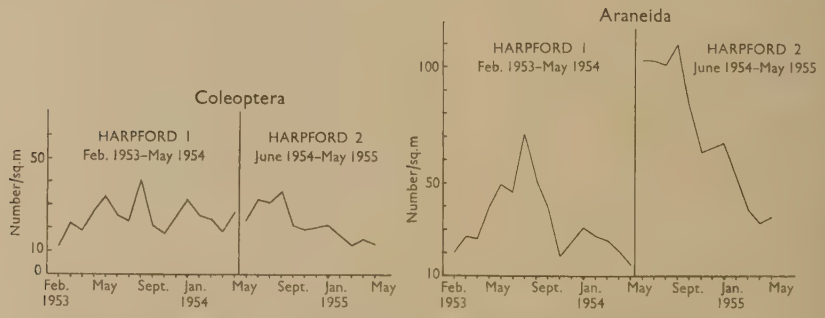

Fig. 4. Density of the Coleoptera and Araneida collected at Harpford.

Harpford 2 with twenty-one common to both sites. Of the twenty-one shared species, *Drassodes* sp. juveniles, *Oxyptila* sp. juveniles, *Lycosa lugubris*, *Lycosa* sp. juveniles, *Robertus lividus*, *Monocephalus fuscipes*, *Microneta viaria*, *Centromerus dilutus*, *Macrargus rufus*, *Leptyphantes zimmermanni* and *L. flavipes* were at a sufficiently high density to be considered important as predators. Only *Phrurolithus festivus* and *Lycosa amentata* were at all frequent of the twenty-eight additional species taken at Harpford 1 and only *Diplocephalus latifrons* important amongst the nine additional species taken at Harpford 2.

Eleven species of Chilopoda were present at Harpford 1 and nine at Harpford 2. The seasonal variation in total centipede density is shown in Fig. 5. *Lithobius duboscqui* was the most common species at Harpford 1 and *Schendyla nemorensis* more frequent at Harpford 2 with *Lithobius variegatus* tending to replace *L. duboscqui*. *Geophilus carpophagus* was relatively common at both sites.

The Pseudoscorpiones *Chthonius ischnocheles*, *Neobisium muscorum*, *Microcreagris cambridgei* and *Roncus lubricus* were recorded from Harpford 1 and all but

the latter at Harpford 2. The seasonal variations in total pseudoscorpion density are shown in Fig. 5. *Chthonius ischnocheles* was the most common species, but at Harpford 2 *Neobisium muscorum* was partially replaced by *Microcreagris cambridgei*.

After desiccation in the funnels, the litter on the trays was carefully removed, sorted and weighed. The litter was composed of oak leaves, beech leaves, twigs (various, but mainly oak) and a little soil and also a mixture of beech mast, acorns,

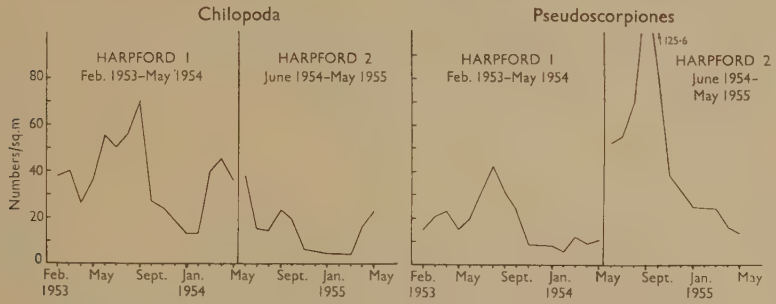

Fig. 5. Density of the Chilopoda and Pseudoscorpiones collected at Harpford.

pine needles and other debris. The seasonal changes taking place in the composition of the litter at the two sites and changes in the percentage composition are shown in Fig. 6. Oak leaves formed the largest single component of the litter at both sites. There is a pronounced peak in October-November due to the autumn leaf fall and the lowest level is reached the following July-August immediately before the next leaf fall. The other components remain relatively constant

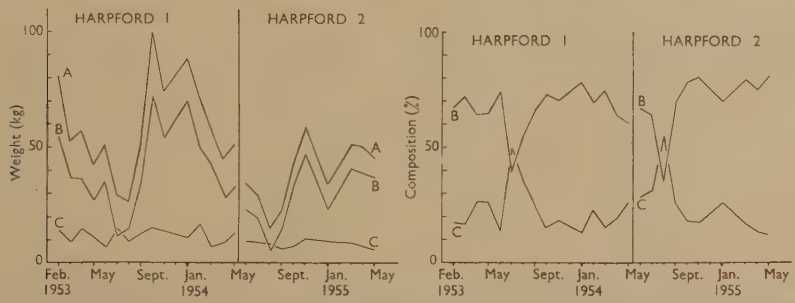

Fig. 6. The composition of the leaf litter collected at Harpford 1 between February 1953 and May 1954, and at Harpford 2 between June 1954 and May 1955: *a*, by weight; *b*, as percentages. A, total weight; B, oak leaves; C, twigs.

throughout the year. The amount of soil present is usually less than 10% per collection which indicates that very little of the mineral soil layer was removed during sampling. The percentage increases in the weight of twigs in July-August reflects the fall in the oak leaf component. The litter at Harpford 1 had a higher mean weight per sample (almost twice that at Harpford 2) but oak leaves made up a greater percentage of the total weight at Harpford 2.

The density of four predatory groups, Coleoptera, Araneida (Fig. 4), Chilopoda and Pseudoscorpiones (Fig. 5) exhibits seasonal changes. The months in which the population peaks occurred, are shown in terms of number per unit area in Table 19.

Table 19. *Months of peak population*

	Peak in numbers/sq. m		Peak in numbers/100 g of oak leaves	
	Harpford 1, 1954	Harpford 2, 1955	Harpford 1, 1954	Harpford 2, 1955
Coleoptera	September	September	July	August
Araneida	August	September	August	August
Chilopoda	September	September (?)	July	August
Pseudoscorpiones	August	September	August	August

It has already been shown that the oak leaves are the major and variable component of the litter over the year. By calculating the number of animals per 100 g of oak leaves it is possible to obtain a rough estimate of the concentration or dilution of the predatory fauna. It is assumed that the use of this parameter gives an indication of the 'living space' available because of the relation between leaf weight and litter volume. This relationship is not constant, however. Soon after leaf fall the leaves lie free from one another so that for a given weight, the volume enclosed

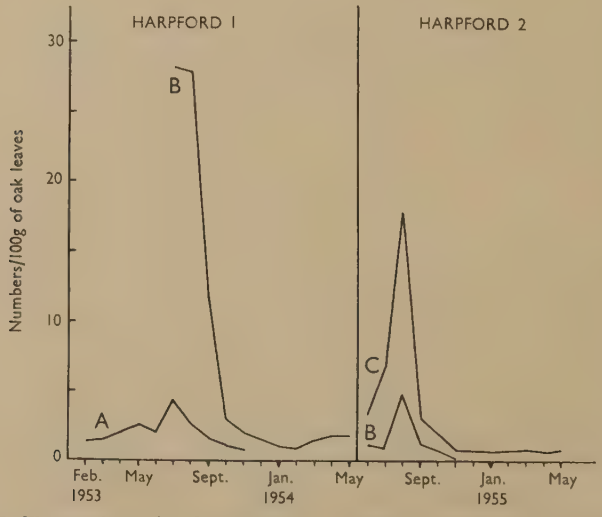

Fig. 7. The numbers of each generation of *Nemobius sylvestris* per 100 g of oak leaves at Harpford. A, B, C, 1951, 1952 and 1953 generations respectively.

by the litter reaches its highest value. As the year proceeds, the leaves tend to become compressed and disintegrate so that the enclosed volume probably reaches a minimum value in July-August.

The months in which the population peaks occurred, in terms of numbers per

100 g of oak leaves are also shown in Table 19. These peaks, therefore, coincide with the lowest level of the litter and precede the peak numbers per unit area by 4-8 weeks. Thus the maximum predatory effect is probably exerted before the maximum number of predators is reached.

The peak numbers of *Nemobius* per unit area occurred in August and September for the 1952 generation at Harpford 1 in 1953 and in August for the 1953 generation at Harpford 2 in 1954 (Fig. 1). The peak numbers per 100 g of oak leaves occur in July-August and in July respectively (Fig. 7). The hatching period and the build up in the *Nemobius* population, therefore, takes place at a time when the predatory fauna is at its highest concentration. As these predators have been observed to eat *Nemobius* in the laboratory, it is suggested that mortality in the population can be attributed to them.

DISCUSSION

In view of the contradictory evidence, it is difficult to assess the role the litter plays as a place in which to live and as a food source. Touratier (1951) shows that nymphs prefer oak leaves whilst Neubar (1937) and Rober (1949) report that they have only collected this cricket from beech litter. In view of the undoubted omnivorous habit of *Nemobius* it may be that the litter provides a suitable place in which to live, the food requirements being of secondary importance. In this case microclimatic factors may be important. Alternatively, if food requirements are critical, different populations may be confined to and utilize different types of litter. There appears to be a superabundance of food if the availability and accessibility of litter at the different levels are discounted. In southern England the cricket is absent from many accumulations of oak litter so that the conditions for existence involve more than an optimal supply of food. The relationship of the *Nemobius* to the litter must be complex and it follows that the interaction of the climate, the particular type of litter and its suitability as a food source, soil type and the previous distribution of the species are all conditions necessary for the existence of the population.

There is a marked difference between the numbers and the species of predators found at Harpford 1 and 2, and there is a genuine difference between the litter samples at the two sites although the low soil content indicates that the samples are relatively homogeneous. The higher density of most of the predators at Harpford 2 coincident with a low weight of litter and a reduction in the number of species present suggests that no simple relationship exists between the litter and the predators. The differences can be accounted for in terms of the quantity and quality of the litter, the efficiency of the turn-over by the reduction in the number of trophic levels at which energy is lost (Birch & Clark 1953), and the ultimate balance achieved between the predators and the herbivorous groups.

Since it appears that the litter is not edible immediately after leaf fall, there is a lag between leaf fall and the nutritional optimum of the litter. It is possible that most species are unable to utilize the litter until the following spring as a result of the low winter temperatures. If *Nemobius* is typical of the herbivorous fauna then

the peak populations occur before the litter reaches its lowest level. This coincides with the time at which the predators are at their greatest concentration and they subsequently build up their peak populations at the time of leaf fall. This brings about a dilution of the whole fauna correlated with which there is a decrease in predation. Van der Drift (1951) shows that in beech litter the fauna retreats to the deeper layers of the litter seasonally and in times of drought, and stratification of the fauna occurs. In oak litter, owing to its comparatively quick decomposition, there are no layers representing accumulations from previous years, and faunal stratification is less marked.

The method of sampling precludes an objective assessment of the distribution of *Nemobius* in the litter. Subjective impressions are that it lives in the topmost layers of the litter during the summer, and somewhat deeper in the winter. The accessibility and availability of *Nemobius* as a food source for the predators may be limited by different spatial distributions (*e.g.* Geophilidae) but in most cases the predators are able to move rapidly throughout the litter and hence are able to prey upon *Nemobius*.

In England, the insect exhibits annual cyclic isolation as a result of a strict univoltine life cycle which includes the diapause and an over-wintering instar. Each generation only breeds once and the chances of overcoming the isolation have been shown to be negligible. In the two generations collected, at any one time, there exists no direct interdependence of density. Mortality factors affect each generation separately and the greatest mortality follows hatching.

Considering a single generation (the 1953 generation at Harpford 1) it is probable that 20% mortality occurs in the egg stage. The reliability of this estimate, in the field, is uncertain as it was deduced from laboratory cultures. No egg parasites were found and presumably mortality at this stage is due to non-viability factors. If both the first and second spermatophores (Gabbutt 1954) are required for a successful fertilization then non-hatching may be a result of incomplete fertilization.

Two factors may cause mortality at the time of hatching; soil texture and wetness. The former may be relatively unimportant in all but loose soils but the latter undoubtedly causes the death of the vermiform larva and first instar in flooded laboratory cultures and might be expected in the field. High precipitation resulting in an increase in the free water in the soil and litter cavities must then adversely affect the percentage hatch.

The build-up of the nymphal population occurs at a time when the predators are at their greatest concentration. These predators have been observed feeding on *Nemobius* in the field and in the laboratory and it is presumed that mortality is a result of their action.

In France, *Nemobius* has a 1-year life cycle and it is interesting to speculate on its probable relationship with the associated predatory fauna. The litter cycle is similar to that encountered in this study but most of the eggs hatch in September-October when the amount of litter present reaches its highest level. This suggests a fundamental difference in the distribution of mortality throughout the whole of the life cycle. Alternatively, if the distribution of mortality is approximately the

same in the two populations and if this is accounted for by predators then significant differences are to be expected in the structure and timing of the predatory peaks in France.

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Permission to work at the sites was given by the Principal of the East Devon Agricultural School, Bicton, and the Rolle Estates, Exmouth, and I am grateful for their co-operation. The work was undertaken whilst in receipt of a Nature Conservancy grant to the University College of the South-West, Exeter.

SUMMARY

1. The life history of the wood cricket, *Nemobius sylvestris* (Bosc.) has been studied in three populations in oak leaf litter in Devon.

2. Eggs laid August-November go into diapause until spring.

3. Instars 1-5, distinguishable by head-width, are present in summer and autumn; the fifth normally over-winters. Instars 6-8 are present in spring and reach maturity in August.

4. The insect breeds once a year and the generations are distinct. Since the life cycle lasts 2 years, there is annual cyclic isolation in the three populations studied. Different cycles have been reported elsewhere.

5. Growth-rates estimated from head-widths are significantly described by linear regressions.

6. Two periods of growth are separated by a winter pause. Growth-rate differences were insignificant between the sexes, significant between generations, but not correlated with temperature or rainfall.

7. The lengths of the stages, date of hatching and length of the hatching period were calculated.

8. Fecundity was estimated from field and laboratory experiments.

9. The sex ratio is unity.

10. Mortality data have been fitted to a logarithmic regression. Mortality is approximately 20% in the egg, 67% on hatching, and 11% over the first growing period.

11. The insect is omnivorous but eats mainly fallen oak leaves, which form

the largest single component of the litter, with a peak in October-November and a minimum in July-August.

12. Predators ate the first five instars of *Nemobius* in laboratory experiments.

13. Predators reached their highest concentration, but not greatest numbers, when the *Nemobius* population was at its peak.

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EAGLES, LAMBS AND LAND MANAGEMENT ON LEWIS

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Arising from a complaint by the head keeper and shepherd at Morsgail, Uig, Isle of Lewis, that golden eagles (*Aquila chrysaetos*) had been killing his lambs in the spring of 1954, a report was submitted to the Department of Agriculture for Scotland by one of its Senior Inspectors. This report suggested that on the evidence examined there appeared to have been an increase in the number of eagles in the Uig district in recent years and that lambs were being taken in considerable numbers. It recommended that a fuller investigation should be made, covering the island as a whole. The Nature Conservancy deputed one of its Scientific Officers to conduct the inquiry and invited Mr David Stephen to work with him. They were on the island together from 16 April to 31 May after which there was no suitable occupied eyrie left available for watching. Mr Stephen returned to Lewis towards the end of June to investigate an eyrie which the party had previously failed to locate, but which had been found and protected by a shepherd. The eyrie, which was easily accessible, contained one eaglet; it was visited by Mr Stephen on five occasions between 18 and 24 June.

In order to locate occupied eyries and thus determine the number of birds present, a search was made in all areas which, from experience gained on the mainland of Scotland in previous years, seemed likely to be suitable. This work was greatly assisted by a map supplied by the Department of Agriculture showing a number of sites where eagles were believed to breed. Useful information was also given by certain islanders (Appendix II).

As things turned out, only two occupied eyries were available for watching and at neither could a hide be built. Moreover, one of these eyries was destroyed when the eaglets were 2 weeks old. In place of watching from hides, regular visits were made to the nests and all new prey noted on each occasion. In view of the shortage of occupied eyries, greater weight had to be given to food remains in unoccupied nests than had initially been intended. It may be noted that it was planned to remove every lamb found in an eyrie and to send it for post-mortem examination to determine the cause of death. For each lamb so removed rabbits to the same weight were to be placed in the nest; this would prevent the eagles being put under more pressure to kill lambs than they would have been without such interference. To this end, arrangements were made for supplies of rabbits to be flown to Lewis

as necessary. In fact, it proved unnecessary to send any lambs for post-mortem examination since only one corpse, obviously killed by an eagle, was obtained.

BACKGROUND TO THE PROBLEM

(*a*) *The availability of wild prey*

The rabbit (*Oryctolagus cuniculus*) is unevenly distributed throughout Lewis, the main concentrations being on the machairs where the density is often high. Few rabbits were seen on the hill and there mostly amongst rocks; there were few typical burrows. Myxomatosis had not reached the island.

During the whole period spent on Lewis the investigators saw only three mountain hares (*Lepus timidus*). According to Mr Ferguson, keeper on Morsgail Estate for fifty years, the hare began to disappear from Lewis in 1946-7, where previously it had been abundant. Rabbits became scarcer on the hills about the same time.

The distribution of the rat (*Rattus norvegicus*) in Lewis is uncertain but it is understood to be common on certain small islands, *e.g.* Vuia More, and perhaps also on the shore, near crofting communities.

Red grouse (*Lagopus scoticus*) are thinly distributed in Lewis; they breed about 3 weeks later than on the mainland. In the course of 2 days spent on Ben Bragor only three birds were flushed, but as it is stated that grouse on Lewis characteristically lie close, this figure may be misleading as a guide to numbers.

The golden plover (*Charadrius apricarius*) is widely distributed and common; during May it was seen and heard daily in every part of the island. There are few curlew (*Numenius arquata*) and dunlin (*Calidris alpina*) but snipe (*Capella gallinago*) are numerous throughout the year, as are woodcock (*Scalopax rusticola*) in the late autumn and winter. The hooded crow (*Corvus cornix*) is plentiful, and so is the raven (*C. corax*).

(*b*) *The availability of mutton carrion*

The mortality of sheep and lambs in Lewis is high. Although the winter of 1954-5 was exceptionally severe, sheep losses were considered locally not to be much greater than usual, so that the conditions observed during the period of the survey can be regarded as fairly typical. The island as a whole is heavily over-grazed and much of it is quite incapable of supporting adequately the animals upon it. To illustrate the extent of the mortality suffered, twenty-eight dead sheep (ewes and hoggs) were counted on a two-mile transect of Ben Bragor on 20 April and three dead ewes were seen on the same day on the roadside between Morsgail and Garynahine. Lamb mortality is much higher than would be accepted on the mainland, many of the losses being due to failure of the ewes' milk supply. The ewes suffer from deficiency diseases and have to be cast early, because they lose their teeth: their horns breaks off also. Only one flock in this area is tended by a full-time shepherd (an unusual feature in a crofting community): the owner of the sheep claimed that the lamb crop averaged 80%, of which only 10% were lost.

This is an exceptionally favourable return for Lewis, where in most cases the loss appears to be much higher. Darling (1955, pp. 230-7) shows that there has been an immense rise in the numbers of sheep in Lewis and Harris; in 1946 the livestock, mainly sheep, was 40% more than in 1911; also the ground is seriously overgrazed and burned, and this maltreatment of the land is reflected in a drop, to about 65% by 1944, of the number of lambs surviving annually per 100 ewes.

FIELD OBSERVATIONS

(*a*) *The number of eagles involved*

It is believed that at the lowest figure there were either seven or eight pairs of eagles in Lewis in 1955. There were certainly no fewer than this and there may have been two additional pairs on the Lewis-Harris border where fresh kills were found and birds were seen, but actual proof of nesting was not obtained. In addition, there was an undetermined number of immature birds, two being definitely located. The distribution of the pairs was as follows: north-east Lewis, one pair; Bragor, one pair and one immature bird; Lochs, two or three pairs; Uig, three pairs and one immature bird, despite the fact that two pairs were shot here in 1954.

The number of eagles in the Uig district is high by mainland standards. On roughly 70 000 acres there were three pairs of eagles and one immature bird. A considerable part of the area (about 20 000 acres) is barren of sheep, rabbits, hares and grouse, whilst parts of the more fertile coastal strip are too heavily populated for eagles to hunt. For these reasons, each pair of eagles probably occupies on the average an effective hunting area of not much more than 10 000 acres in country in which wild life is for the most part very sparse. Watson (1958) records fourteen pairs in 220 square miles or one pair per 10 000 acres in the north-east highlands. He points out, however, that not all of these areas were used by eagles. In Wester Ross (Lockie, unpublished) three pairs occupy approximately 39 000 acres or one pair per 13 000 acres. In both these areas, and especially the first, wild prey is more plentiful than on Lewis. In this same area of Uig there were four pairs of eagles nesting in 1954 and probably either three or four pairs in 1953. According to Mr Ferguson, former keeper at Morsgail, eagles began to increase in Lewis about 1946. This increase has been confirmed by Dr J. W. Campbell (personal communication).

(*b*) *Nesting success*

Out of four eyries watched in the Uig and Bragor area in 1955 only one reared a single eaglet to the flying stage. At the second, the two young birds vanished from the nest when about 2 weeks old, almost certainly removed by human agency. No eggs were laid in the third eyrie, where one of the pair disappeared at an early stage and the freshly lined nest was abandoned. At the fourth eyrie, there is some evidence that the birds were deliberately kept off the nest, which was inaccessible and impossible to see into. Eggs may have been laid but no young were raised.

The three or four eyries in east Lewis were not visited by the survey party. The three known nests were on an estate where no lambs had been lost to eagles and for this reason and because access was difficult attention was concentrated on the complaint area in the west.

(*c*) *The food of eagles on Lewis*

The following information is summarized from lists of prey remains observed at, or taken from, seven sites occupied by eagles either in 1955 or in previous years, or both. Some of these sites had several eyries. Details are given in Appendix I.

The food brought to the two eyries occupied in 1955 consisted in order of frequency of rabbits, grouse, golden plover, hares and rats; no lamb remains were found. One of these eyries is known to have been occupied in 1953 and 1954. According to the shepherd and the proprietor the food in 1955 was similar to that noted in the previous 2 years. No lambs were found at the nest in either year. The remains of prey identified from three unoccupied eyries was in order of frequency rabbit, sheep wool, grouse, lamb (wool and bones), rat, crow, raven and adult red deer.

The method of study tends to minimize the occurrence of grouse and exaggerate the occurrence of lamb, for whereas grouse can be almost completely digested, the bones of lambs remain and are conspicuous. The presence of lamb bones in an eyrie is not, of course, proof that an eagle killed the lamb. At one eyrie last occupied in 1953, the remains of two lambs were found. The keeper had, however, visited the eyrie regularly and was satisfied that the lambs had been brought to the nest as carrion. Both Arnold (1954) and Murie (1944) record adult eagles feeding on carrion during the nesting season.

During our stay an immature bird hunted over the complaint area in Morsgail in which a pair of eagles had been destroyed in 1954. Two kills, both rabbit, were seen and six pellets collected; all six pellets contained rabbit or hare fur, one sheep wool, one lamb wool and one feathers. This bird also attacked two live lambs, one of which died; the other survived with a gashed flank. No evidence was obtained from any other quarter of lambs having been killed (see Appendix II for information from local residents).

Two sites were visited on the Lewis-Harris border. Eagles were present but no proof of breeding was obtained. Four kills were found on the cliffs, all rabbit. At two other sites sixteen undated pellets and rabbit bones were collected. Fourteen of the pellets contained rabbit or hare, three sheep's wool, two unidentified feather and one grouse.

DISCUSSION

From the remains found at eyries it is clear that rabbits are the main prey of eagles on Lewis. Lambs and sheep are also eaten and the diet is supplemented by a few hares and grouse and by occasional rats, golden plover and hooded crows. The remains of lambs found at unoccupied eyries do not in themselves indicate

whether the lambs were killed by the eagle or whether they were picked up after death. However, bearing in mind the considerable losses of lambs in most years by starvation and the report by one sheep-owner that the two lambs brought to an eyrie in his ground were carrion, it seems likely that most lambs appearing in eyries are carrion. And in fact lamb killing has only been demonstrated on one estate, Morsgail. It may well be that the eagles on this estate are especially short of wild prey.

Eagles began to increase in Lewis about 1946 at approximately the same time as mountain hares and grouse (and rabbits on some hills) began to decline. The reason for the decrease of hares, grouse and rabbits is not known; it may have been associated with an increase in the number of sheep on the ground. The density of eagles in 1955 was similar to that in the eastern Grampians, an area much richer in wild life than Lewis, and it seems likely that an alternative food has become available to compensate for the decrease in wild prey. This, we suggest, is lamb and sheep carrion. There is an apparent parallel in the Pecos district of west Texas (Arnold 1954). Here the shepherding of sheep and goats is inadequate, grazing pressure varies from heavy to extremely heavy and land use may be abusive and wild prey is scarce. Eagles are nevertheless abundant, and it seems probable that they are attracted to the area by the continuing availability of mutton and goat carrion.

Under these circumstances the shooting of troublesome birds cannot solve the problem. Their place will be taken by newcomers. Improved land use, in contrast, would permanently right the balance which has been so violently upset by man. Until that is done the high flock-mortality will continue to perpetuate the present artificially high stock of eagles by ensuring their food supply.

ACKNOWLEDGMENTS

The following land-owners gave permission for us to work freely on their estates: Mr Robinson, Morsgail; Barvas Estate Co. Ltd. (per F. G. Baird); Uig Crofters Ltd. (per N. MacKinnon, Tarbert); Sir T. O. M. Sopwith, C.B.E., Amhuinnsuidh, north Harris; Brocket Estates Ltd. (per N. MacKinnon); Mrs MacKenzie, Scaliscro; Miss Thorneycroft, Eishken, and Grimersta Fishing Syndicate (per J. Gillies). The following keepers and others helped greatly with information and discussion: John Gillies, Grimersta; Malcolm MacDonald, Morsgail; Duncan Macrae, Eishken; Louis MacDonald, Scaliscro; Kenneth MacDonald, Reef; and F. MacMillan, Barvas. In addition, we acknowledge the kindness and hospitality of the people of Lewis with whom we came in contact. We are indebted to the Director of the Wool Industries Research Association, Leeds, for identifying, as far as is possible, the wool and fur in eagle pellets, and to Dr A. S. Clarke, Royal Scottish Museum, Edinburgh, for identifying the bones obtained in unoccupied eyries and in pellets. The report by Mr Sam Isbister, Senior Inspector, Department of Agriculture, provided most useful information on the location of certain eyries. Mr Pat Sandeman and Mr A. B. Duncan provided information about eyries on Lewis. Dr Stamp, Director, Moredun Institute, Edinburgh, agreed

to make a pathological examination of lambs removed from eyries. We had, however, no occasion to take advantage of this kind offer.

SUMMARY

1. A complaint of lamb-killing by eagles on the Island of Lewis was investigated.

2. The food eaten was determined by observing what was brought to two eyries and by analysing the pellets and bones found in old eyries.

3. Rabbit was the main food eaten. Lamb-killing occasionally occurred but many dead lambs and sheep were also available.

4. Eagles began to increase about 1946 at the same time as hares, grouse and, in places, rabbits decreased. The stocks of sheep, however, which had been considerable, were further increased beyond the capacity of the habitat to support them; as a result there have been considerable annual spring and winter losses.

5. This carrion, it is suggested, is maintaining an artificially high density of eagles and other carrion feeders. Any pest tendencies of eagles which may occur from time to time will not be solved permanently by shooting but would be by improved land use.

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APPENDIX I

FOOD IDENTIFIED IN EYRIES ON LEWIS

Site 1—west Lewis

(*a*) Prey found at nest after eggs hatched, 1955.

	In nest	On cliff near by
6 May	2 rabbits, 1 mountain hare	—
9 May	2 rabbits, 1 red grouse	Golden plover, mountain hare
11 May	2 rabbits, 1 red grouse (containing eggs)	Golden plover and leg of hare
13 May	Nest empty.	

(*b*) From occupied eyrie —Pellets 1 and 2, rabbit and hare fur; pellet 3, rabbit and hare fur and foot of red grouse.

(*c*) From old eyrie—Pellets 1-3, rabbit or hare fur; pellets 4-5, sheep and lamb wool. Bones, rabbit; bones, 3+grouse sterna.

(*d*) Roosting place, undated—Pellets 1-11, rabbit or hare fur; pellets 12-13, sheep wool. Bones, 2 rabbits.

Site 2—west Lewis (reared young 1953)

(*a*) Bones of 2 lambs, at least 5 rabbits, 1 rat, 1 hooded crow, 1 raven, 3 red grouse.

(*b*) Pellet 1, rabbit fur and some sheep wool; pellets 2-4, wool of sheep and lamb, rabbit fur; pellet 5, sheep wool; pellets 6-9, rabbit; pellet 10, rabbit, rat(?); pellet 11, lamb wool, rabbit, deer hair; pellet 12, rat, rabbit; pellet 13, rabbit, feathers; pellet 14, rat fur, some sheep wool; pellet 15, bird; pellet 16, undetermined fur; pellet 17, undetermined fur, some sheep wool.

Of the 17 pellets 15 contained fur, 8 wool, 2 bird, and 1 deer hair. Of the 8 pellets containing wool, 3 had fibres suggesting lamb. The deer hair was that of an adult animal.

Site 3—Beinn Bragor

From roosting place referred to March 1955—pellet 1, rabbit or hare fur, some sheep wool and feathers; pellet 2, mainly rabbit or hare fur, possibly some wool; pellet 3, grouse (?), fragments of limb bones of a small bird.

Site 4—Morsgail estate, west Lewis

(*a*) From eyries occupied before 1955—pellets 1-8, rabbit or hare fur; pellet 9, sheep wool, some undetermined fur; pellets 10-11, lamb and sheep wool; pellet 12, undetermined. Various bones of one lamb and of one rabbit.

(*b*) Kills and pellets of immature eagle, 1955—Two rabbit kills; pellets 1-4, rabbit or hare fur; pellet 5, lamb wool, some fur and feather; pellet 6, sheep wool and some fur.

Site 5—Lewis-Harris border

Three rabbit kills and one pellet containing rabbit or hare fur.

Site 6—north Harris

One fresh rabbit kill found on cliff.

Site 7—west Lewis

This eyrie successfully reared young in 1953, 1954 and 1955. The prey noted in 1955 was as follows:

(*a*) During May by L. MacDonald (shepherd) on successive visits—rat, rabbits, rabbits, nil, golden plover.

(*b*) During June by D. Stephen—18 June, 2 rabbits, grouse feathers; 20 June, 1½ rabbits; 21 June, 2 rabbits; 23 June, 2 rabbits, 1 rat; 24 June, 1 rabbit.

Note: This was occupied in 1953 and 1954 when the eagles successfully reared young. According to the shepherd who visited the nest in both years the food was similar to that found in 1955. No lambs were brought to the eyrie.

APPENDIX II

The following is a summary of the information obtained from crofters and others on Lewis concerning attacks by eagles on lambs.

Malcolm MacDonald, Morsgail, who made the original complaint in 1954, states that in that year he saw five attacks by eagles on lambs before the breeding eagles were killed. In 1955 he saw one attack on a live lamb and found the remains of another which the investigators agreed had been killed by an eagle; he also saw one lamb being carried off but the cause of death was not established. In all these cases the same (immature) bird was concerned. Mr MacDonald considers that the behaviour of the eagles on this ground in 1954 and 1955 was exceptional; he has no complaint against eagles in general and does not subscribe to the view that eagles normally attack live lambs.

Kenneth MacDonald of Reef, an official of the Uig Crofters Grazing Committee, has never seen an eagle attack a live lamb. He knew of one instance where an eagle had been flushed from a newly killed lamb by a neighbour of his, Mr Morrison. Mr Morrison, when interviewed, stated that he had indeed put an eagle off a lamb a fortnight before, but the lamb was cold and had not been killed by an eagle. The only other time that Mr Morrison had put an eagle off prey was from a rabbit.

Mr MacDonald, 15 Reef, a farmer on the Machair, had a number of still-born lambs this year;

others died of lack of milk. A few of his lambs had disappeared and had not been accounted for, but he had never seen an eagle attacking a live lamb or carrying off a dead one. He considers the great black-backed gull (*Larus marinus*) to be the major threat to lambs.

Mr Ferguson, former keeper at Morsgail, stated that before 1946-7, when eagles began to increase, he had never known an eagle take a lamb; now, he maintains, he has seen a lamb attacked in the early part of the lambing period.

John Gillies has been keeper at Grimersta for 20 years. He has never known an eagle to attack a lamb either in Lewis or on the mainland of Kintail. He has seen his ewes grazing regularly beside an occupied eyrie but has had no losses to eagles. In July 1954 he flushed an eagle from the carcase of a ewe by the roadside; he put an eagle, presumably the same bird, off the carcase on his return journey the same day. It is his opinion that the eagles of Lewis eat mainly rabbits and carrion. Until 1954 he never heard any complaint of lamb-killing.

Finlay McLeod, Enaclete, a crofter, has a few sheep on the common grazing between Morsgail and Grimersta. He estimates that the crofters have about forty lambs in this area. Lambs are lost every year from many causes – drowning, falling into holes, accidents, disease, etc. The chances of finding the bodies are remote. He had no information of eagles killing lambs. He confirmed the high mortality of adult sheep.

Admiral the Hon. E. R. Drummond of Garynahine heard no complaints of lamb-killing until 1954. He has lost no lambs himself and is doubtful if attacks by eagles are common. He flushed a buzzard from a lamb four years ago; the lamb was warm and had wounds on its neck.

Duncan Macrae (70) is head stalker of Eishken Forest and has spent all his life there. His father was head stalker before him for 30 years. He has never known an eagle to take a lamb and is doubtful if lamb-killing by eagles is more than exceptional. Miss Thorneycroft, the owner of Eishken Forest, confirmed her head stalker's statement.

W. J. MacDonald, butcher, has a sheep farm at Barvas. His shepherd is not troubled by eagles. He has 'thousands of rabbits' on his ground.

Mr McLeod, keeper, Kinloch Resort, who is over seventy and has been on the ground most of his life, stated that he had never seen an eagle taking a live lamb, nor met anyone who had. Nevertheless he is convinced that eagles do kill lambs.

The shepherd of Aline, Loch Seaforth, who works a sheep run up to Craig na Lubaig, says that eagles are always about the Rock. He believes they attack lambs, but has never seen this happen. He regards buzzards as a greater menace to lambs than eagles.

SUMMARY

Out of thirteen people interviewed, two only, Mr Malcolm MacDonald, the complainant at Morsgail, and Mr Ferguson, his predecessor on the same estate, had seen eagles actually in the act of attacking lambs. Mr MacDonald saw this happen five times in 1954, after which he shot the birds, and once in 1955, when a second lamb clearly killed by an eagle was found also. His 1955 observations were confirmed by the two investigators from the Nature Conservancy. None of the other eleven people interviewed had any evidence of eagles attacking lambs; two of them nevertheless believe that they do so.

SOME INTERSPECIFIC RELATIONS BETWEEN JAPANESE AND EUROPEAN HONEYBEES*

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(With Plate 1 and 6 Figures in the Text)

Two species of honeybee occur in Japan, the native species, *Apis cerana cerana* Fabr., and the introduced one, *A. mellifera* L.† Ancient Japanese apiculture was practised exclusively with the former, which still inhabits the mountainous regions either living wild or in primitively reared conditions. Since the first importation of *A. mellifera* from the United States in 1876, modern apiculture which uses this species exclusively has spread rapidly, and today the majority of colonies kept in Japan belong to it and are mostly of mixed strains, with a distinct predominance of the Italian race, *A. mellifera ligustica* Spinola. This co-existence of two originally allopatric species presents several problems interesting from both biological and apicultural standpoints, but of these only two will be considered in the present paper.

The first is the problem of artificially mixed heterospecific colonies, a classical problem in the study of ants but little mentioned in the social bees until the recent work of Nogueira-Neto (1950). Such investigations produce valuable data on specific differences of ecology, behaviour, etc., which serve as a basis for the study of the second problem, interspecific competition in the field.

With respect to the relationship between two species possessing similar biological requirements, many ecologists support the validity of Gause's principle, which postulates that such species cannot permanently co-exist in one and the same habitat, unless their increase and the resulting competition are prevented through certain environmental factors. However, the criticisms which Andrewartha & Birch (1954) have raised against this principle must be remembered, especially the scarcity of direct proof and the need for further accumulation of empirical data.

In this study, the mixed colony problem will be considered first, and since direct evidence of interspecific competition in the field is from the nature of the problem difficult to obtain, my own observations will be augmented by those of experienced beekeepers. Even so it must here be stressed that much further research is needed. The relationship between two allied species varies according to whether they interbreed or not. A hybrid strain between *A. mellifera* and *A.*

* Studies on the Japanese Honeybee *Apis cerana cerana* Fabr. VI. Contribution No. 407 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

† On the adoption of these scientific names refer to Sakagami & Akahira (1958). On the specific difference between two species see Sakagami (in press). Both species will henceforth be abbreviated *C* and *M* respectively.

cerana has occasionally been reported in India (*e.g.* Vats 1953), but in spite of repeated efforts made in Japan, no hybrid has so far been obtained between *A. mellifera* and *A. cerana cerana* (Hachinoe, personal communication). On the other hand, an observation by Matsuda (personal communication) suggests that interbreeding may not always be out of the question, but the situation is as yet obscure and further studies are required. It is certain, however, that under natural conditions these species interbreed only very rarely if at all.

MIXED COLONIES

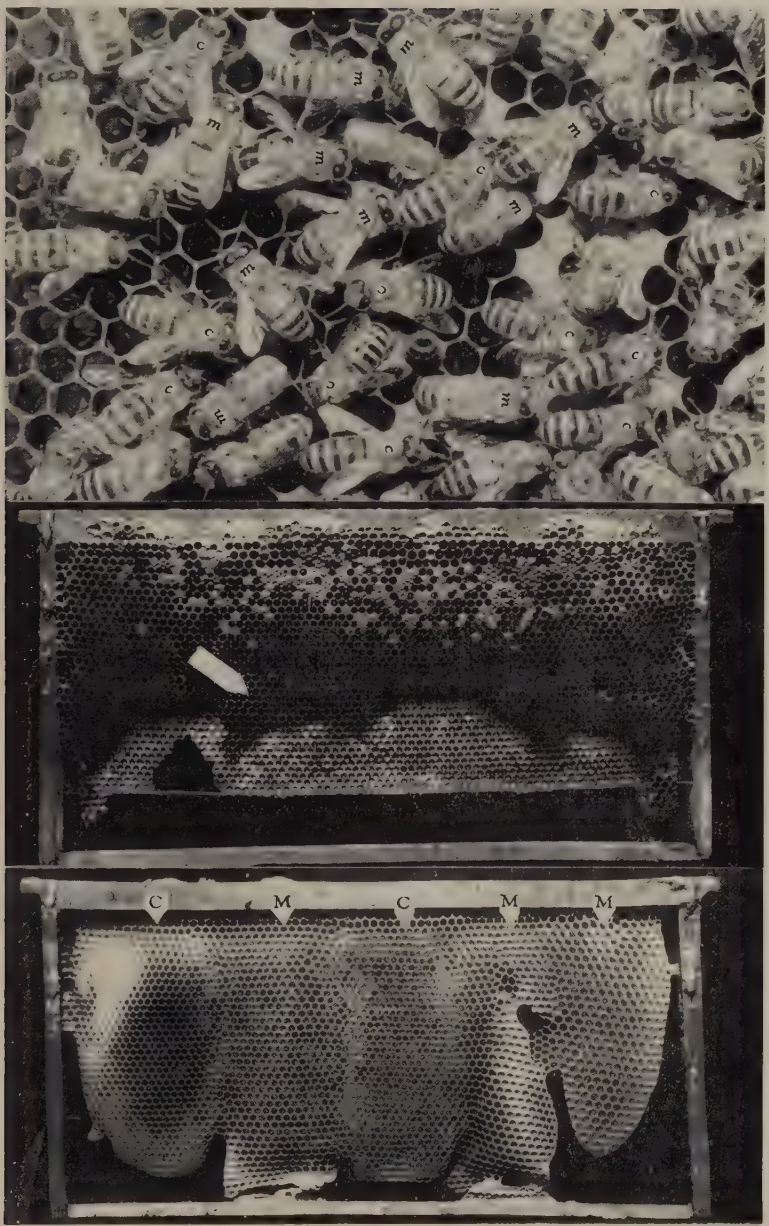
(*a*) *Mixing of young individuals*

If workers younger than 3 days after emergence are used, mixed colonies can be prepared very easily. The life history of such nuclei will be described elsewhere. Here it is only necessary to mention that, in such circumstances the workers of both species completely tolerate each other, intermingle indiscriminately, and co-operate for the maintenance of the colony (Pl. 1*A*). Provided the nuclei are started with about equal numbers of both species, further young bees of either type can be introduced with little trouble. However, such harmony can break down as a result of physiological changes in the constituents. In one mixed queenless nucleus ovary development and accompanying aggressiveness (Sakagami 1954) appeared after a peaceful co-existence lasting 10 days. Attacks were both inter- and intra-specific but most severe by *M* towards *C* and within 2 days all the *C* workers were expelled. A similar event was also observed in another queenless nucleus, but in this case severe aggression was directed by *C* towards *M*, and it did not reach expelling intensity.

The transplantation of young *M* workers into *C* hives was very easy. In 1953 and 1955, a total of about 700 *M* workers was collected just at emergence and introduced into *C* hives. They were hardly attacked at all by the nest owners and the two lived peacefully together. Some workers were used to determine whether the *C* queen can inhibit the development of *M* worker ovaries or not. For this purpose, *M* workers were taken about every 3 days from a *C* hive, and even up to 30 days after introduction there was no lack of material to be examined. This proves distinctly that the introduced *M* workers may remain alive in *C* hives for about as long as in their own.

On 11 June 1955 fifty *M* drones which had just emerged were introduced in a *C* hive and on the next day thirty more. On the fourteenth day after introduction, about twenty were observed in the hive, showing little sign of maltreatment. Therefore, it is concluded that the young *M* individuals are easily adopted by *C* colonies.

On the other hand, the reverse transplantation (of young *C* workers into *M* hives) was extremely difficult. In 1953 and 1955, from June to September, about 220 newly emerged *C* workers were introduced into *M* colonies. The nuclei of the adopting colonies generally consisted of only two or three combs as the smaller colonies are probably less aggressive than larger ones. Even though the introduced *C* workers were smeared with honey collected from the combs of the adopting



A: A heterospecific nucleus consisting of *Apis mellifera* (*m*) and *A. cerana cerana* (*c*) mixed soon after emergence.
B: A *mellifera* comb given to a *cerana* colony. The lower parts were gnawed down. The arrow indicates the parts repaired by *cerana*.
C: A mosaic comb built first by *cerana* (C), then by *mellifera* (M). Compare Fig. 2*b*.

(*Facing page 52*)

colonies none were found when the nuclei were examined on the next day; and moreover, most were driven out immediately after their introduction.

To confirm the effect of scent conditioning in the adopting colonies, about 200 newly emerged *C* workers were confined to the queen cages; each cage contained ten bees and was placed between two central combs of *M* colonies. After 3 to 8 days, they were released into the colony in which they had been confined. However, on the next day only five *C* workers could be found. Two of these had disappeared on the third day but three others survived much longer and could be observed until the eighth day after release. Two of them survived until the seventeenth day when they were taken out from the hive for another purpose.

Similarly 165 newly emerged *C* drones were released into *M* hives after 1 to 2 days' confinement in the queen cages. When the hives were inspected 1 hour after their release from the cages, none were found. For comparison about 150 newly emerged *M* workers were taken from two *M* colonies, marked with coloured paint, and confined to the cages each containing ten bees. The cages were placed in a *C* hive for from 5 to 8 days and the bees were then released into *M* hives other than their own. Of 104 bees released more than seventy-five individuals were found on the next day, more than fifty on the seventh day after introduction, and about seventeen on the thirty-fifth day. Therefore, it is clear that these *M* workers, even after their stay in *C* hives during their juvenile period, could survive in the strange *M* colonies for as long as in the home colonies.

The results may be summarized: 1. The introduction of young *C* workers into *M* colonies is far more difficult than the reverse case. 2. Once accepted, even *C* workers can survive for quite a long period in a heterospecific colony. 3. The difference of toleration seems to lie in the specific differences of odour and aggressiveness.

(*b*) *Drifting of* C *workers into* M *colonies*

In spite of the difficulty in transplanting young *C* workers into *M* colonies, it is often observed that the *C* workers live in *M* colonies without apparent sign of maltreatment. On this point, some observations by experienced beekeepers and by myself will be described briefly.

On three occasions Matsuda (personal communication) observed the mixing of whole colonies (twice in June, once in July) when *C* swarms invaded *M* hives. Each time the hive owners showed no defensive action and the members of the two colonies were found intermingled on the combs. It was amazing to observe the fanning activities in such mixed colonies. At the hive entrance the two species showed fanning activity side by side, according to their specific pattern: *C* workers fanned against the entrance and *M* workers towards it. Each time the *C* workers gradually disappeared but twice there was a strange occurrence in the following year. Although the size and colour of the next year's workers were intermediate between *C* and *M*, they showed certain characteristics of *C* such as a marked congestion on the comb, a peculiar confusion, loud communal hissing and pertinaceous crawling on the back of human hands at inspection. As mentioned in the

introduction, this indicates the possibility of interbreeding between the two species, though it is hard to explain why such individuals appeared after 1 year.

Kouta (personal communication) observed an unusual case of the drifting of individual *C* workers into an *M* colony. An *M* colony, situated about 4 m from a *C* colony suffered mild robbery by *C* workers. After the home colony of these *C* robbers had been moved some distance away, some joined the former victim colony, and of 8000 workers in this colony, 10% were found to be of *C*, living amicably with the *M* ones.

Drifting between the two species is, however, most frequently observed immediately after the translocation of one colony into the vicinity of the other. On 25 July 1953 a medium-sized *C* colony was sent to our laboratory from Shiga Prefecture. Some of the workers drifted into an *M* nucleus situated near by. On 28 July about forty *C* workers were seen intermingled in a nucleus with *M* workers and the former showed little sign of maltreatment. The number of drifted *C* workers decreased to thirty-three on 1 August and to twenty-two on 12 August. This reveals that they can sometimes survive in *M* colonies for a considerable time.

In order to observe artificially induced drifting, a *C* colony from the original site was replaced on 5 June 1955 successively by two *M* colonies (*Ma*, with five combs and a virgin queen; *Mb*, with three combs and a fertilized queen). This took place from 12.00 h to 14.50 h and the homing *C* workers were found to be absorbed into either of these two *M* colonies.

The result is summarized as follows:

		Ma	*Mb*
5 June	12.00 h		Placed in *C* site.
	12.30	Placed in *C* site.	Returned to the original site.
	13.00	Returned to the original site.	*C* guards appeared at the entrance. Both *C* and *M* guards inspected *M* and *C* homing bees.
	13.30	*C* guards appeared. Inspection of both *M* and *C* homing bees.	,,
	14.30	Again placed in *C* site until 14.50.	
	15.00	*C* and *M* about equal in number. *C* more aggressive than *M*. At the entrance, 64 *C* and 24 *M* were dead. *M* queen was attacked by her own workers.	*C* and *M* about equal in number. *M* queen was attacked by *C* workers.
6 June	9.00	Only 22 *C* workers. Both *M* and *C* guards at the entrance. Queen was safe. Several attacks *M* v *C*.	*C* occupied about two-fifths of the total number. Queen safe but wing tips and left-hand tarsi absent.
		Several *M* begged to *C*.	Several attacks of both *M* v *C* and *C* v *M*. Some *C* workers in the royal court.
	12.00	Only 10 *C* workers. No *C* guards. Several attacks of *M* to *C*.	
	15.30	Only two *C* workers, mauled by *M*.	

On 7 June *C* workers could still be found in *Mb*, but not in *Ma*. Thereafter the *C* workers in *Mb* decreased gradually but could still be observed until 30 June.

Therefore it was shown that *C* workers occasionally drift into *M* colonies either

as a total swarm or individually. These intruders are usually attacked and expelled by the hive owners, but may be tolerated and survive for a considerable period in the *M* colonies.

(*c*) *Behaviour of both species in the mixed state*

The attitude of the hive owners towards the introduced bees is similar in either homospecific or heterospecific transplantations. They approach with extended antennae and fore-legs and then they grasp the introduced bees with the legs and begin to examine each other with vibrating antennae. If the introduced bees are smeared with a small quantity of honey, the inspectors may either take this food first, or continue mauling as if no honey smell was perceived. Often these two drives occurred simultaneously, the tongue being extended for licking the honey and the mandibles moved for the attack. The further behaviour of the examiner and examined is divided into four categories: combat by mutual aggression, unilateral dominance, indifference, and amicability as shown by regurgitation. Naturally, in introducing young bees, the combative situation does not occur, because of the lack of fighting drive in young bees. But it is noticeable that combat seldom occurred even when the mature adult workers of both species were encountered, as in the drifting of *C* into *M* or vice versa. Or if it did occur, the combat changed rather quickly into unilateral dominance. The full exposition of mutual aggression is therefore seen only at the hive entrance, or when both species encountered each other away from the hives and nest-mates.

The behaviour of *M* workers, which have been accepted in C colonies, differs little from that of the nest owners. It is noteworthy, however, that *M* guards in a *C* colony usually inspected the incomers and attacked the drifting bees much more severely than the *C* guards. Moreover these tolerated *M* workers in *C* colonies showed a stronger aggressiveness than the *C* workers to the further introduced young *M* bees.

The *C* workers which were accepted in *M* colonies, either by introduction at the juvenile period or by drifting, participated in both the house and field duties. They were not usually seen in the centre of combs, but on the top-bar or in the marginal area. *C* workers seem to avoid *M* comb. Most *M* workers were either indifferent or rather amicable towards the tolerated *C* workers, but some of them consistently attacked the adopted workers. This differential aggressiveness (Lecompte 1954, Sakagami 1954) is assumed to be one of the main causes of the difference between the fate of the drifted *C* workers in different *M* colonies.

The initial phase of mixing between *C* and *Ma* or *Mb* colonies was very interesting. In both colonies the *C* guards appeared at the hive entrance less than 30 min after mixing. From the procedure taken it is highly probable that most of these *C* guards were the foragers immediately before mixing. Actually, one *C* guard foraged actively for more than 30 min, leaving the full pollen loads in her corbiculae. Butler & Free (1952) mentioned that guards could appear quickly when the colony was alerted. The present example illustrates fairly well that in cases where there is great confusion, even the foragers participate in guard duty.

The inspection and attack at the entrance was most frequent and severe by *C* to *M*, next by *M* to *C*, and frequently by *C* to *C* and *M* to *M*. In every case, the attacked bees showed no sign of resistance.

From the above description, it was shown that unilateral dominance occurs frequently. The behaviour of two individuals in this situation is strictly identical to the description of Butler & Free (1952) and Sakagami (1954). The attacked individual shows little resistance, usually strops her tongue, and often enters into a 'hypnotic' state (cf. also Grozdanič 1951). The inter-individual attitudes were always very definite, even when the small *C* worker attacked the more robust *M* one. Such unilateral dominance was also observed in the various mixed colonies of the stingless bees (Nogueira-Neto 1950), when the two species co-exist relatively peacefully. Therefore, among the higher social bees, there seems to be a releasing mechanism which elicits, either innately or after experience, the submissive attitude of those attacked.

(*d*) *Exchange of* C *combs between two species*

The comb of one species was repeatedly, after removing the attached bees, inserted into the hive of the other species. The combs of both species were of the ordinary Langstroth type. In Japan, *C* are usually kept without removable frames. This species shows a marked dislike of an ordinary nest foundation and if given it in the usual way will gnaw it. I therefore took Dr Y. Tokuda's advice and gave them a frame in which the foundation was only 2-3 cm in height, enough to give them the first orientation for construction (Fig. 2). Even with such frames, they showed a marked rejection of the foundations. If *C* combs of this kind are inserted into *M* hives, they are always welcomed as is shown by the following example:

21 July 1955	A *C* comb containing sealed and unsealed honey, pollen and all the development stages was inserted into a medium-sized *M* colony.
22 July	Comb intact. Contents were apparently intact, except that there was a considerable degree of egg destruction.
23 July	Sealed brood intact, the unsealed brood remained. Two newly emerged *C* workers were attacked by *M* workers.
24 July	Newly laid *M* eggs, characterized by their erect form, were seen throughout the comb. The queen was in the act of laying. Sealed *C* brood was intact. There were no newly emerged *C* workers although there would have been hundreds if *M* workers had not interfered.
26 July	Except in the stored food area, most of the cells were filled with *M* brood which later emerged safely.

Generally speaking, if a *C* comb is inserted into an *M* colony, the unsealed brood is pulled out, but the sealed brood remains intact until expelled after emergence. The comb itself is fully utilized for storing and brooding, although the cells are smaller than is usual in *M* combs.

On the other hand, the insertion of *M* combs into *C* colonies shows a remarkable contrast to the above case. If an *M* comb was inserted on the outside of the outermost comb of a *C* hive, it was either ignored or partly gnawed down. If inserted between the central combs, the stored food was accepted, and the unsealed

immature stages were not driven out 'intentionally' but succumbed because of the absence of subsequent care. The sealed broods were tolerated and later emerged safely, but the comb itself was always gnawed down from the lower parts and if this destruction reached the brood area, the *M* brood was gnawed indiscriminately with the comb wall. The cell walls were gnawed down until the foundation plane was exposed and in most cases, the damaged parts remained in this condition (Pl. 1*B*). Occasionally cells were re-built on this exposed base up to the normal height (Pl. 1*B*, arrow), and if such were used at all it was generally for pollen storage (Fig. 1, 24 Sept.), but in most cases they remained unused. The diameter of these repaired cells corresponded to the original foundation structure, so that although they had the diameter of usual *M* cells they were in fact *C* cells. The fate of an *M* comb inserted in a *C* hive is shown in Fig. 1.

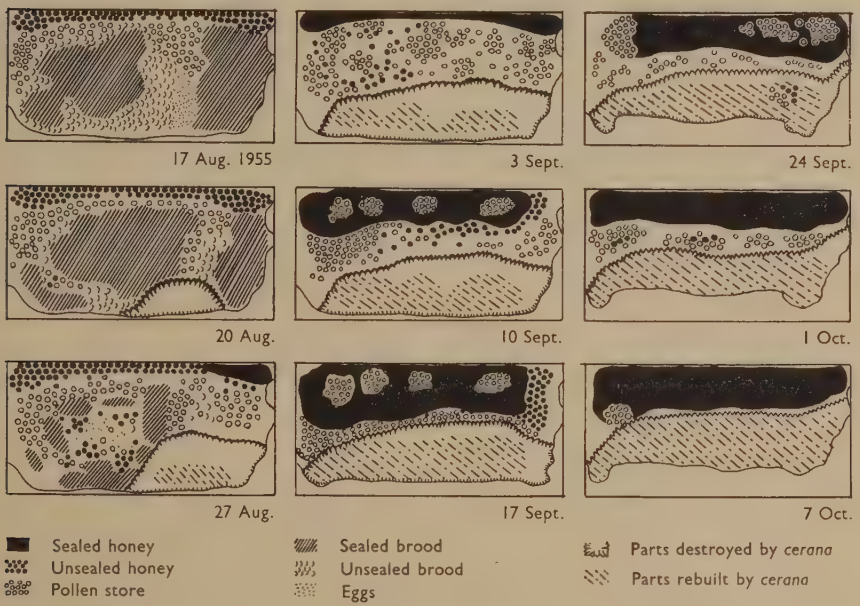


Fig. 1. The gradual destruction of a *mellifera* comb by *cerana* workers.

Another experiment was made in order to show the difference between species with respect to comb insertion. On 30 June 1955 a standard Langstroth frame was inserted in a *C* colony. The frame was provided with a foundation plate with three rectangular incisions (Fig. 2). The *C* workers accepted this frame, and started building on the fifth day after insertion. They built, however, only in the two foundation-free areas (Fig. 2). On the twenty-second day after insertion, these two areas were approximately completed, but *C* workers did not build in the areas provided with a foundation. The foundation was partly gnawed down or modified as seen in Fig. 2. Thirty-three days after the first insertion, the comb

was taken from the *C* hive and put into an *M* hive where it was immediately welcomed by *M* workers. The immature stages of the *C* workers were thrown out and oviposition began in these small cells. Moreover they began to add to the comb on the thirty-seventh day after the first insertion into the *C* hive. Thus a

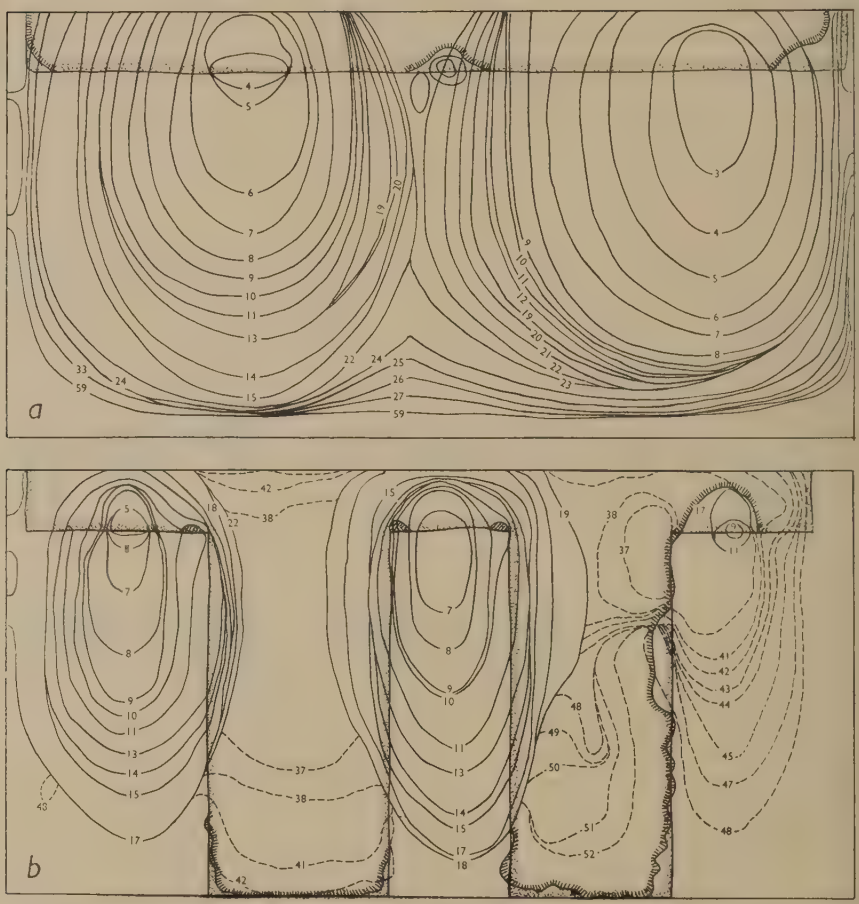


Fig. 2. *a*, The process of comb building in a Langstroth frame given to a *cerana* colony. Punctured and striated contours show the margin of comb foundation (soon after insertion, and after modification by *cerana* workers, respectively). Solid contours represent the area built in the *n*-th (numerals indicated) day after insertion.
b, The process of comb building in a Langstroth frame with incised foundation. The comb was first given to a *cerana* colony (solid contours), then to a *mellifera* one (broken contours).

mosaic comb was built up, first by *C*, then by *M* workers (Pl. 1*C*). In this *M* hive, the parts made by *C* workers were repeatedly utilized as the brood areas.

Therefore, the two species behave in a diametrically opposed manner towards the inserted heterospecific combs. The *M* workers welcome the *C* combs but

refuse the *C* broods in them. The *C* workers destroy the *M* combs from below together with any immature stages which may be there.

INTERSPECIFIC RELATIONS AS INTERCOLONIAL PROBLEMS

(*a*) *The relative aggressiveness and strength under confinement*

This problem occupies a transient position between the mixed colony problems already described, and intercolonial relations. Throughout the above observations, it was seen that *M* workers behave much more aggressively and inimically than *C* ones. How then, do these two species behave if they are placed in confinement? For this problem, the following small homo- or hetero specific assemblages were confined in a wooden box, $10 \times 10 \times 5$ cm, with a glass lid: *M* 10, *C* 10,

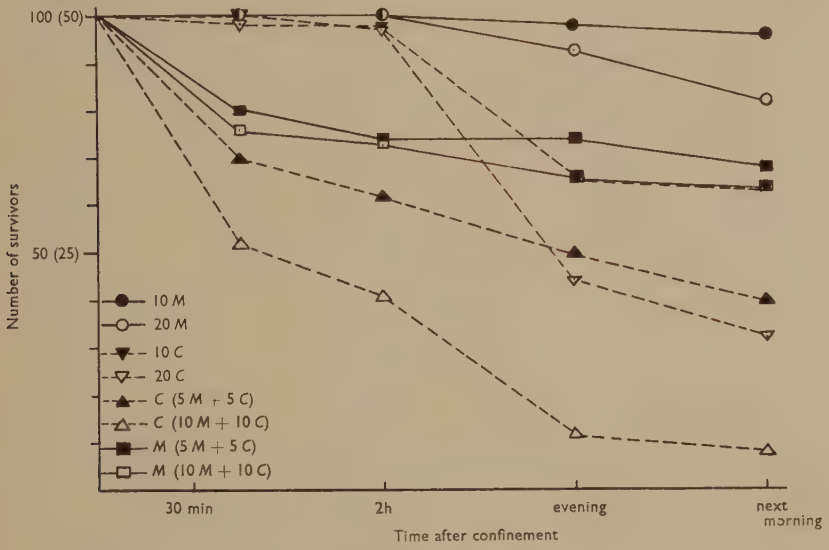


Fig. 3. The decrease of surviving workers confined homo- or heterospecifically.

M 5+*C* 5, *M* 20, *C* 20, *M* 10+*C* 10. The number of surviving individuals were counted after 30 min, after 2 h, at the end of the day, and on the next morning. Each treatment was repeated five times. The results (Fig. 3) show a higher survival of the smaller groups than of the larger ones, and of *C* workers than of *M* workers, both irrespective of homo- or heterospecific conditions.

The first result is interesting but not related to the problem now under consideration. The second result shows the physical weakness of *C* workers under the given circumstances. However, in all the heterospecific confinement cases a rapid decrease in individuals is seen after the first 30 min of confinement, and most of the interspecific combats were seen during this initial period. The more rapid decrease of the *C* workers than of the *M* ones in this period indicates their handicap in fighting.

For closer observation of relative fighting ability, a flat box of $5 \times 2 \times 1$ cm with a glass cover was prepared as the contest arena. The box was divided into two sections by a middle partition and in each section, one worker of each species was placed. The partition was then removed, and the process of the interspecific encounter observed until it brought a distinct result, or for up to 10 min if there was no fighting.

The results of this experiment, which was repeated fifty times with a renewed combination of the two species, are difficult to classify into distinct categories, but may be summarized as follows:

1. In twenty-six trials, severe fighting was observed, in which six *M* and twelve *C* workers were stung, and two *M* and ten *C* died.
2. The degree of relative aggressiveness was about equal in twenty-one trials; $C > M$ in eighteen and $M > C$ in eleven.
3. The initial attack was made by *C* in twenty-five trials, by *M* in twelve, and about simultaneously by both individuals in four.
4. In seventeen trials unilateral dominance was observed, by *C* in twelve trials, *M* in four trials, and reciprocally in succession in one trial.
5. In six trials regurgitation was observed; *M* fed *C* in three trials, and vice versa in three others.

Therefore, the relative aggressiveness was, unexpectedly, stronger in *C* than in *M* under these conditions, but combat brought the victory of *M* more frequently than that of *C*. The greater aggressiveness of *C* is explained by the difference of excitation, for after confinement in the box, most of the *M* workers walked to and fro excitedly, especially upside down underneath the glass cover (this seems to be caused by the higher photic sensitivity of *M* than *C* workers—phototaxis as an escape device; *cf.* v. Buddenbrock (1952), p. 67) and these movements of *M* caused *C* to attack, although previously they had remained relatively quiet on the bottom of the box.

The result of a combat is ultimately determined by the difference in muscular tensions, whereby the successful worker can prevent the other from stinging, at the same time promoting its own sting. The general muscular power was distinctly superior in *M* than *C*, except the biting power. Actually *M* would in many instances inhibit the stinging act of *C* by the use of their legs. *C* could not do this so effectively, though the powerful mandibles of *C* counteracted, to a certain degree, their general inferiority. This mandibular power was shown repeatedly by the difficulty of separating *C* from *M*, even after the death of the former. It is clear that this ability relates to a specific tendency of *C* to gnaw the hive wall, old combs, the confined box, and the hands of men manipulating the nest.

(*b*) *Occupation of the feeding place by* M

To observe the interspecific relation at a common feeding place, the following experiments were undertaken six times. With two colonies, *M* and another *C*, the bees were trained to feed from watch glasses filled with sugar syrup, placed on the alighting board. Then, two glasses were gradually shifted from the hive entrance, and simultaneously brought closer together. The two watch glasses were visited by the foragers of both species, owing to their nearness. The end

results were, however, invariably monopolization by *M* as is seen in one example (Fig. 4). Although at first the individuals from the two species did not attack one another, they gradually began to do so, and finally *M* did not allow *C* to take the syrup. The *C* foragers persistently attempted to thrust themselves into the ring of *M* foragers sucking the syrup, but the attack of *C* by *M* was much more successful. In each case three to five *C* but no *M* foragers were killed by the combat. Having had the two watch glasses side by side, one was removed, when *M* foragers showed a typical territorial defence reaction and did not allow *C* even

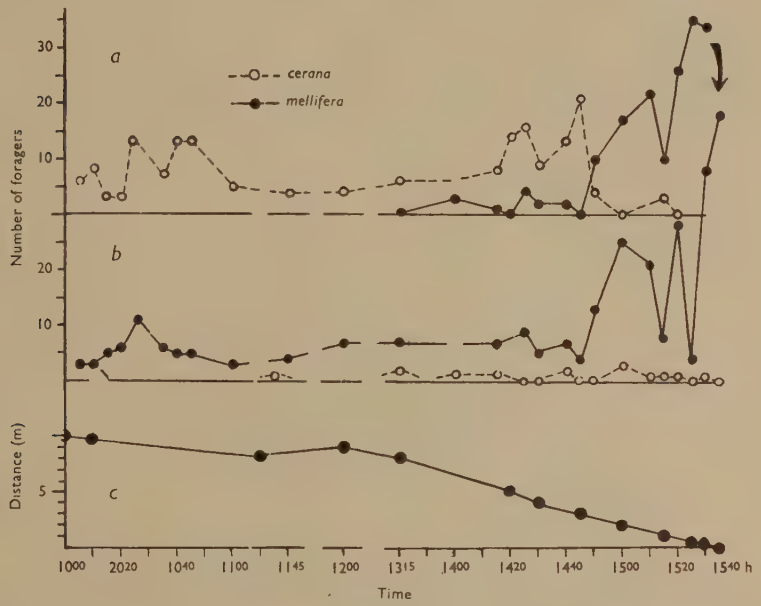


Fig. 4. Process of the monopolization of feeding places by *mellifera* foragers. The graphs show the numbers of foragers of each species *a*, at the feeding place for *cerana*, *b*, at the feeding place for *mellifera* as the distance, *c*, between the feeding places was reduced. At the end (arrow) only one feeding place remained.

to approach the feeder. Curiously enough the bees most severely attacked by *M* were the *M* workers which had been transplanted into the *C* colonies soon after emergence.

(*c*) *Robbery between two species*

Nogueira-Neto (1949) divided robbery in the social bees into two categories: 'mild pillage' that was usually carried out by a small number of thieves and often continued for a considerable time, and 'exterminating pillage' involving a larger number of thieves. Both types are recorded in *M* and *C* colonies, but the mild pillage of *M* upon *C* colonies usually develops into the exterminating kind. Behaviour of robber bees is characterized by a peculiar swaying flight at the hive

entrance; the swaying flight of an *M* robber bee, at the entrance to a *C* hive is figured (Fig. 5). The *C* guards pay less attention to the robber bees than the *M* guards; usually they show only a slight turning accompanied by the abdomen-shaking characteristic of the species. During the first 5 min six *M* workers entered the *C* hive practically without resistance and returned home with full crops. Also *C* has a distinct pillage tendency. The mild pillage of *M* colonies by *C* is characterized by its pertinacious attachment to the victim colonies (Kouta, Fukushima, Kamikawa, personal communications). The *C* workers once centred around a definite *M* colony are not easily chased away. This house-fly-like behaviour was conclusively observed by me, when a few *C* workers visited a strong *M* colony.

The exterminating robbery of *M* by *C* is, according to Fukushima, not unknown but very rare, and occurs only when the latter are very weak. On the other hand, the reverse case is very frequent. Various bee journals, up to the present published in Japan, contain numerous fragmentary articles on the extermination of *C* colonies

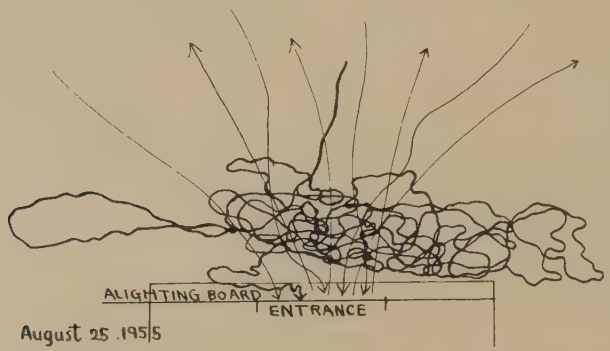


Fig. 5. Flight course of a *mellifera* robber during 46 seconds before the entrance of a *cerana* colony. Fine lines show the flight course of *cerana* foragers.

by *M* robbers. Hattori told me that, in Kagoshima Prefecture, many *C* colonies were exterminated by *M* in the honey dearth, even if the thieves and the victims were separated by more than 2 km from one another. Fukushima met more than fifty such exterminations during his 40 years' apicultural experience. Kouta informed me that *M* colonies tend to attack *C* ones more frequently where there are other *M* colonies in the vicinity.

I twice accidentally observed this catastrophic robbery by *M* of *C*. In both cases the following sequence took place: *C* workers showed little resistance; hence most of the inter-individual contests changed rapidly to the unilateral dominance of *M* to *C*; *M* workers which had been transplanted into the victim *C* colony soon after emergence showed a more marked resistance than *C* ones, to the conspecific robbers; and within 1 h after the initial attack, the *M* robbers occupied the victim colonies. The surviving *C* workers escaped in a swarm. This coincides in general with the observations made by many experienced beekeepers. It was very interesting that in one of the above cases, the *M* guards which came

from the robber colony, occupied the entrance and crevices of the victim colony, and inspected their comrades.

Generally speaking, it is very difficult to rear two species concurrently in the same apiary. It results eventually in the robbery of *C* by *M*. The victim colonies are either completely exterminated or they escape in an absconding swarm. The

Fig. 6. Gradual replacement of *cerana* by *mellifera* at the foot of Mt. Yatsugatake.

Circled M show the *mellifera* apiaries established since the years indicated. Circled C are the last records of *cerana*-swarm catches at the given locality. Double-circled C are reared *cerana* colonies with the records of their extinction or continuation. Oblique striations represent the approximate flight ranges of both species and their overlap.

survival of the escaped refugees may not be successful, although they may construct a secondary nest owing to their excellent wax secreting ability. The robbery occurs, however, mostly in the autumnal honey dearth period. Hence subsequent colony revival is very difficult. Therefore, the exterminating robbery by *M* of *C* colonies is considered as an important interspecific relation between the two species.

(d) Decrease of C *colonies due to* M *under field conditions—a case study*

The decrease of *C* colonies approximately corresponds to the increase of *M* ones throughout Japan. According to Tokuda (1924) the colony numbers of both species reared in Japan were *C* 44 946 and *M* 58 865 but earlier, in 1913, they were *C* 84 997 and *M* 48 054. The subsequent change is hard to obtain, because of the lack of sound statistics on *C*, but this is mainly due to the fact that the rapid decrease of *C* colonies in comparison with the increase of *M* reduced the importance of estimating the colony numbers. It is very probable that this decrease is at least partly caused by the interspecific competition between them. However, it is extremely difficult to determine exactly how much the direct interspecific encounter gave rise to this gradual replacement of *C* by *M*. Here one example is cited, in which the gradual replacement is fairly distinctly shown.

This was surveyed by Mr Kobayashi of our laboratory in 1927 at the foot of Mt. Yatsugatake, Nagano Prefecture, central Japan. Formerly there were many *C* colonies being reared in this district. The first introduction of *M* colonies in 1911 resulted in the total extermination of *C* in the vicinity in the following year, owing to the intense robbery by the former species (Fig. 6). Thereafter, the further establishment of *M* colonies caused the gradual decrease of *C*. At present *C* colonies below 1000 m above sea level remain only in one locality, where they have been reared since before 1927. Even at the higher altitudes the number of swarms caught by a lure-hive decreased (Fig. 6). This retreat of *C* into higher altitudes seems to be caused not only by interference-type competition (the exterminating robbery) as in urban districts, but also by the exploitation around the nectar sources. Conclusive evidence cannot be obtained with respect to the relative importance of these two types of competition.

DISCUSSION

Amongst social insects, heterocolonial enmity is, even if conspecific, a universal rule. In ants, the tolerance of heterocolonial individuals is seen only exceptionally (*Lasius fuliginosus*, Stumper 1953; *Formica rufa rufopratensis minor*, Gösswald 1951). In the social Apoidea Hockings (1884) showed a specific difference of intercolonial tolerance in the stingless bees. In the honeybee, artificial mixing is relatively easy in comparison with other social insects, and is actually undertaken as an apicultural procedure. On heterospecific mixing, various mixed colonies were made in ants either by the mixing soon after emergence or antennectomization (Fielde 1903-5) or by the sudden change of environment (Brünn 1912). In the social Apoidea, the problem was recently studied extensively by Nogueira-Neto (1950) using stingless bees. He divided the mixed colonies into three categories, the permanent, the relatively peaceful, and the impossible. The present case shows, however, that there are occasions in which the relation between two species can cover all three categories. Here the relationship was a permanently peaceful one in the mixing of young workers or in the introduction of young *M* into *C* hives, relatively peaceful in the occasional drifting of *C* into *M*

hives, and almost impossible in the introduction of young *C* into *M* hives. Thus, the relative tolerance between two species varies considerably according to the given circumstances.

The degree of tolerance may depend on the occurrence of specific difference, ability to discriminate, and aggressiveness based upon this discrimination. It is clear that the differences of odour play the most important part in this. Fielde reported the participation of both inherent and acquired odours in ants. On the other hand, in the honeybee, the difference of colony odours was mainly studied from the standpoint of the acquisition of a secondary odour, doubtless due to the lack of opportunity in comparing the different species in the genus *Apis* (v. Frisch & Rösch 1926, Kalmus & Ribbands 1952, Ribbands 1954, 1955, Steinhoff 1948). The present results show that, at least between *C* and *M*, both the acquired and inherent odours must be considered. The role of the inherent odour is best shown by a comparison of the difficulty in introducing *M*-conditioned *C* young into *M* colonies, with the successful introduction of *C*-conditioned *M* young into conspecific, but alien *M* colonies. On the other hand the comparison of the latter case with the severe attack by *M* of the *M* workers transplanted into *C* hives soon after emergence, shows the role of the acquired odour. Thus the relative importance of both components is complicated and again depends on the situation. This is shown also by the different results in the drifting of *C* into *M* colonies. Kaltoven (1951) ascertained that bees can discriminate intercolonial differences of acquired smell but not of body odour. However, at least in the case of *C* and *M*, it is clear that discrimination is due to the body odour, because the youngest bees, which possess no acquired scent, were used in the heterospecific transplantation.

With respect to interspecific combat, *M* usually took the dominant position in both aggressiveness and agility, though the aggressiveness can be reversed under confinement. Moreover, it was realized that unilateral dominance is important in the contest. Tolerance between two species is less than among the heterocolonial workers of the same or different races of *M*. Combat around a common feeding place has been observed by Kalmus (1941) and Glyne-Jones (1953) between two colonies of *M*. The similar situation which I observed gave a clearer result, monopoly by *M*.

How, then, is it possible to relate these two species mutually under natural conditions? As mentioned in the introduction, Gause's principle postulates the impossibility of the permanent co-existence of two species allied in their ecological relationship because of the resulting competition around common resources. Competition can be further divided into two types, exploitation and interference (Brian 1956b, Birch 1957). Both types were repeatedly tested by laboratory experiments, using Protozoa, granary insects, carrion flies, etc. (*cf.* Andrewartha & Birch 1954, Crombie 1946). The results often showed the extermination of one species. Under field conditions, however, direct evidence of interspecific competition is hard to obtain, especially when only exploitation is concerned. Various field records may be conveniently classified into three categories: 1, examples in which the present habitat segregation is more or less explained as the results of

competition which occurred in the past; 2, examples in which two species have a common overlapping habitat, where competition is observed, and 3; examples in which the chronological parallelism between the establishment of an introduced species and the decrease of an ecologically similar endemic one is observed. The present case belongs to this last category.

Most published examples to date belong to the first category, where past competition is, especially in certain cases, very probable, but cannot be directly proved (*e.g.* Lack 1947). Well-analysed direct evidence of competition in nature is very rare, especially when only exploitation is concerned. In interference-type competition, there are a few examples such as Pitelka (1951) on humming birds, and Brian (1956a, b) on ants. There are numerous fragmentary records of the replacement of an endemic species by an introduced one; the relationship between *Rattus rattus* and *R. norvegicus* is perhaps one of the best known. But, again in this category, analysis has been limited. Throughout all the records, including the present one, there is no single case in which the relative importance of competition has been clearly demonstrated quantitatively. As stated by Andrewartha & Birch (1954), further studies are required for the solution of this problem.

In the present case, two species of bees only partly overlap. The introduced *M* is abundant in urban districts, but the endemic *C* is mainly confined to remote areas. Further, there seems to be a difference in the foraging methods of the two species which decreases exploitative competition: *M* have a tendency to concentrate their effort on a major nectar source whilst *C* tend to forage from numerous minor sources (Hachinoe 1954, Akahira, Kouta, personal communications). Accordingly, if competition occurs, it may be only in limited parts of their habitats. Moreover, it must be remembered that the total colony number in Japan means approximately the total number of reared colonies of *M* but not of *C*, for a considerable number of wild *C* colonies still exist. With reference to the decrease of domesticated *C* colonies, the selection exercised by beekeepers is important, especially in the case of those with many *C* colonies (ten to twenty, up to sixty) who changed over entirely to *M*, a form which has the advantage of being adaptable to movable frames. The decrease of *C* colonies which appeared in the government statistics may be largely explained by this.

Considering factors other than competition, however, there are still many records of the gradual decrease of *C* swarms caught by laymen, and the increased extermination of *C* colonies by *M* robbers, concomitant with the increase of *M* colonies (*cf.* Akahira & Sakagami 1958). Therefore, there is no doubt that competition between the two species and the superiority of *M* can be regarded as one factor causing the decrease of *C*, though its contribution cannot be expressed quantitatively.

Finally, a few words on some specific characters of the two species, which may be helpful in considering their relationship. The superiority of *M* is apparent not only in their larger mean colony size and their higher fighting ability, but also in the continuous protection given to them by human beings. Regarding the superiority of *C*, only two points have been cited which may partly explain their survival

under natural conditions. One is their climatic adaptation to this country; *C* usually forage much later in the autumn than *M*, and they can be over-wintered more easily (Kouta, Akahira, personal communications). The other is their negative resistance to their worst enemy, *Vespa mandarinia* Smith, for in Japan this giant hornet exterminates thousands of *M* colonies annually apparently as a result of a battle before the nest entrance, which *C* avoids by retreating within the hive (Tokuda 1924, Fukushima, Akahira, personal communications), an action which saves many colonies from destruction.

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SUMMARY

1. Some observations on the interspecific relations between two species of honeybees inhabiting Japan, *Apis mellifera* L. (introduced) and *A. cerana cerana* Fabr. (endemic), are described.

2. In general, *A. cerana* is more tolerant and less aggressive than *A. mellifera*.

3. It is suggested that robbery by *A. mellifera* plays an important role in the decrease of *A. cerana*.

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A PREDATORY COPEPOD

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(*From the Plymouth Laboratory*)

(With 1 Figure in the Text)

When dealing with the biology and ecology of communities of plankton animals it is common practice, at some stage of the investigation, to separate the community into carnivores and 'others', and to try and establish a relationship. Included in the former category are the chaetognaths, and in the latter, the copepods.

The chaetognaths are indeed carnivorous and can form the major carnivorous component of a plankton community. The copepods, as can be seen from the observations of many investigators, particularly Russell (1934) and including my present observations, usually constitute some 60% to 80% by numbers of a plankton community, and sometimes more. They can therefore be assigned the position of being the legitimate prey of the carnivorous element, including the chaetognaths. However, in my investigations into the plankton communities of the Singapore region, I have observed that, in the case of at least one species of copepod this position is reversed.

The idea that the pelagic copepods feed only on the floating plants has been questioned, the more so as more evidence appears. Lebour (1922, 1923, 1925), observing living plankton animals and examining plankton hauls, showed that some copepods live on a mixed diet; others, namely *Anomalocera patersonii* Templeton and *Labidocera wollastoni* (Lubbock), are predominantly feeders on other copepods. Lowndes (1935) made some most interesting and informative observations on copepod feeding and has done much to dispel '... a fixed impression among many investigators that the Calanoids are in general filter-feeders, that this filter-feeding is more or less automatic, and that the Calanoids in question can exercise no very marked selection'. He notes some ten species of copepods and their feeding, and there can be no doubt that some of these copepods are selective feeders and mainly, if not wholly, carnivorous. Digby (1954) suggests that some copepods are compelled to become carnivorous during the winter months in some temperate areas, when the phytoplankton production is at a minimum, in order to survive. There is, of course, no question of this in the tropical waters of Singapore.

The material from which the present observations were made is the result of a year's collection of plankton, mainly from the Singapore area, the analysis of which is nearing completion. When dealing with preserved material in a study of this sort, as Lebour notes, caution is necessary inasmuch as, owing to the unnaturally

close proximity of the various organisms in a plankton net and bucket, many animals are captured by others in these circumstances, which would not be caught in the open sea. Lebour concludes by saying: 'In many of the organisms examined, however, the nature of the food was so consistent in various hauls and from various localities, that it seems almost impossible to believe that it is merely accidental ...' (1922, p. 644). This is so regarding a species of copepod common in the Singapore plankton for a large part of the year, *Candacia bradyi* A. Scott.

Analysing some hundreds of plankton samples, I have concluded that this species regularly preys on chaetognaths, particularly *Sagitta enflata* Grassi. There

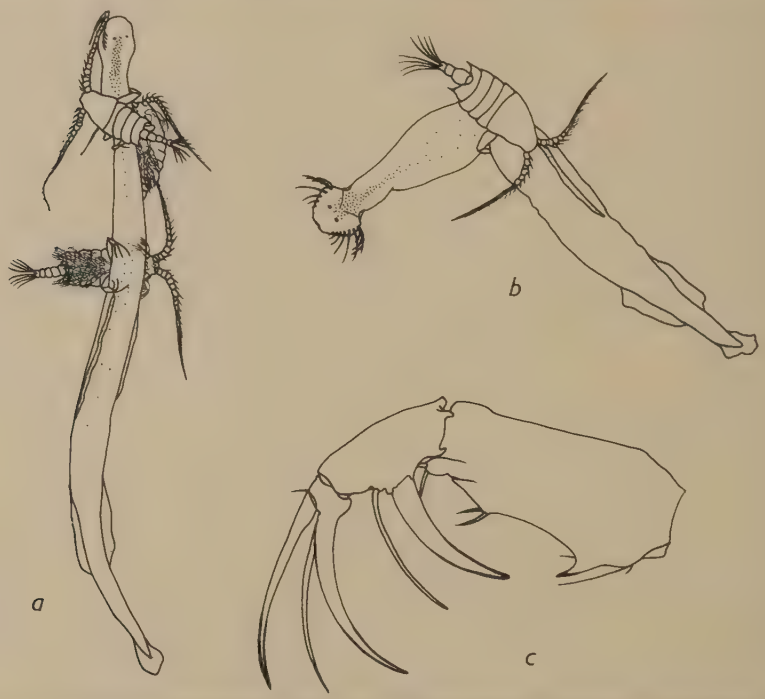

Fig. 1. *a*, *b*, examples of characteristic attitudes of *Candacia bradyi* affixed to a chaetognath; *c*, first maxillipede of a male *C. bradyi*.

may, or may not, be any significance in the fact that this species of *Sagitta* is concerned, since it is generally the most commonly occurring chaetognath in the area and would therefore be expected to form the greatest number of chaetognath victims. However, there is also the point that this species is more flexible than the majority of chaetognaths occurring here, and is therefore more easily grasped by the first maxillipedes of the copepod. As can be seen from Fig. 1 it is the first maxillipedes which assume the most important part in holding the prey. A characteristic of the genus *Candacia* Dana is the development of this first pair of maxillipedes and the reduction of the second.

In *Calanus finmarchicus* (Gunnerus), a copepod which normally filter-feeds, the first maxillipedes possess numerous setae (Marshall & Orr 1955, p. 12). In *Centropages typicus* Krøyer, described by Lebour as a mixed feeder (1922, p. 648) the segmented endopod of the first maxillipede carries long claw-like setae. According to Lowndes (1935, p. 707) there is a well-marked feeding current, but in addition he has observed specimens seizing food by these claw-like setae. Fig. 1*c* is a drawing of a first maxillipede taken from a male *Candacia bradyi* and clearly shows an extreme in its structure. In proportion to the whole animal it is very well developed and the whole structure is more massive than is normally found in a copepod. The three segments of the endopodite are much reduced, the third being almost non-existent, making for greater strength and rigidity. There are definite spines, as opposed to setae, the ends of which are heavily chitinized. Filter-feeding is clearly impossible with such a structure. As a unit, the first maxillipedes have all the essentials of a raptorial organ and can be compared with the raptorial limbs of Stomatopoda. In many instances it was observed that the body wall of the chaetognaths had been pierced by the spines of the maxillipedes.

Examination of gut contents of randomly selected individuals revealed no recognizable plant matter contained within. Thus the facts so far observed clearly indicate that *C. bradyi* is a predominantly, if not wholly, carnivorous copepod. Further, although this copepod has been observed with various other planktonic animals in its maxillipedes, it is clear that in the great majority of cases, as observed in a series of 1/100 sub-samples of the original hauls, it is a chaetognath which suffers attack. It is often the case that several copepods are affixed to a single chaetognath (Fig. 1*a*), four being the maximum number so far noted.

In order to obtain a clearer picture of the selective capabilities of these copepods, two hauls were randomly chosen and the entire contents instead of the normal 1/100 sub-sample were examined. The results are as follows:

Sample 1—Fifty-one individuals were affixed to other animals. Of these twenty-two males and twenty-five females were affixed each to a *Sagitta enflata*, one female to a *S. pulchra* Doncaster, one male to a ctenophore, one male to a juvenile *Eucalanus subcrassus* Giesbrecht and one female to a larvacean. Therefore, of the fifty-one copepods forty-eight (94%) were affixed to a chaetognath, and forty-seven (92%) were affixed to a *Sagitta enflata*. The total numbers of relevant animals in this sample, as judged by a 1/1000 sub-sample of the gymnoplean copepods and a 1/100 sub-sample of the other groups, are: gymnoplean copepods, 51 000; Chaetognatha, 4300; Larvacea, 400; Ctenophora not present in significant numbers.

Sample 2—Twenty-six individuals were affixed to other animals. Of these nine males, six females and one juvenile male were affixed each to a *Sagitta enflata*, two males to a *S. pulchra*, one male to a *S. planctonis* Steinhaus, one male and one female each to a *Diphyes chamissonis* Huxley, one male and one female each to a leptomedusa, one female to a juvenile *Eucalanus subcrassus*, one female to a *Paracalanus aculeatus* Giesbrecht, and one male to an actinotrocha larva of *Phoronis*. Therefore, of the twenty-six copepods nineteen (73%) were affixed to a chaetognath and

sixteen (62%) were affixed to a *Sagitta enflata*. The total number of relevant animals in this sample, as judged above, are: gymnoplean copepods, 54 000; Chaetognatha, 5500; Siphonophora, 4800; medusae, 600; *Phoronis* larvae, about 100. There were no examples of more than one copepod being affixed to a single chaetognath in these samples. Even allowing for the probable fact that the shock of the preservative caused some copepods to relinquish their grasp on some of the animals, and that some of the animals are more easily relinquished than others, there is evidence of selectivity with the feeding of this copepod.

Since this species is one of the more commonly occurring of the pelagic copepods around Singapore, it will produce an effect on a plankton community by directly preying on herbivores, and even more by removing some of the carnivorous chaetognaths. The analysis of the two samples above shows that, in the first haul approximately 1·1% of the chateognaths were attacked by this species of copepod, and in the second haul 0·35%.

It is hoped that the ecological relationships of *Candacia bradyi* will be investigated experimentally by workers in whose area this species of copepod occurs. There is some evidence that another species of copepod, *Tortanus gracilis* (Brady), is an active predator mainly on other copepods, but since this is one of the less common species, observations are not sufficiently numerous to exclude the possibility of chance rather than intent.

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SOME FEATURES OF THE BIOLOGY OF THE TENCH *TINCA TINCA* (LINNAEUS) IN TASMANIA

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(With 8 Figures in the Text)

The tench *Tinca tinca* (L.) is a freshwater teleost found throughout much of Europe including the British Isles. The Report of the Royal Commission on the Fisheries of Tasmania, made to the Tasmanian Legislative Council in 1882, states that tench 'were introduced by the late Captain Langdon, and had permanently established themselves in the still waters of such rivers as the Clyde, South Esk and the Jordan, especially where weeds are plentiful'.

Tench occur today in the South Esk River system (South Esk, Meander, Macquarie, Lake Rivers) in northern Tasmania and in the Clyde, Jordan and Coal Rivers in the south. They are also found in Lake Tiberias, about 40 miles north of Hobart (altitude 1450 ft), which when it overflows becomes joined to the Jordan River. These are the principal Tasmanian tench waters, though there are some other much less important occurrences. In Tasmania the waters where tench flourish are the still and weedy kinds described as favoured by tench in Europe (Yarrell 1841, Lunel 1874, Maxwell 1904).

Although the tench has been reported in fish cultural literature because of its economic importance in some parts of Europe (Schaeperclaus 1933, Mortimer & Hickling 1954), has been the subject of some anatomical and physiological studies, and has been written of rather anecdotally by certain naturalists (Yarrell 1841, Lunel 1874, Maxwell 1904), the biology of wild populations appears to have been little studied. Data on which this paper is based were collected during a study of the use of tench in fish culture (Weatherley 1958). It was easier to assess their success in farm dams against a background of some knowledge of their biology in the wild—especially in relation to food and growth. Fish were trapped in the Coal River and Lake Tiberias, where they were also captured by electro-fishing and hand nets.

PHYSIOLOGICAL EXPERIMENTS

(*a*) *Lethal high temperatures*

Experiments were performed in an aquarium tank $18 \times 12 \times 12$ in. mechanically aerated and heated by means of a partly screened 200 W bulb immersed in the water. A continuously operating stirrer prevented temperature gradients, and the tench were kept below the water surface by a wire screen. Fish from Lake Tiberias and from the Coal River were used, being transferred immediately to the laboratory after capture; experiments were then conducted after as little delay as

possible (one day at most). In the experiment the water was heated up gradually from room temperature until all the fish in a sample had died.

Fig. 1 shows the temperatures at which fish became disabled and died at various times of the year. It will be seen that the temperatures were much higher in summer than winter. This is similar to the seasonal variation Brett (1944) found for a number of freshwater fish species. Hart (1952), Fry, Hart & Walker (1946) and Brett (1944) have also abundantly demonstrated the effect of temperature of acclimatization on lethal temperature, showing that the latter cannot be adequately estimated from experiments performed only at one time of the year or at one acclimatization temperature. Tench used in experiments ranged from 2·7 to 27·5 cm in length and size seemed unimportant within this range in influencing upper lethal temperatures.

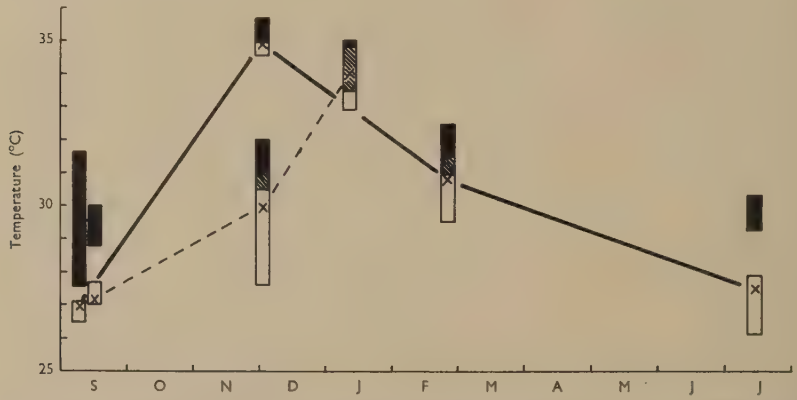

Fig. 1. Temperatures of disablement and death for tench at various times of the year. White columns represent the range of temperature over which fish became disabled; black columns indicate the range over which the disabled fish died; hatched columns indicate where the two overlapped. × signifies the mean temperature of disablement for a given batch of fish; —, fish from L. Tiberias; — — —, fish from Coal River.

In tench the first sign of disablement due to high temperature was slight loss of balance and co-ordination, progressing as the temperature increased. When a fish no longer moved it was considered that its lethal temperature had been reached. But it is believed that the temperature of disablement has the greater ecological significance, since it represents the lowest temperature causing noticeable physiological impairment. During exposure to lethal high temperatures tench behave as follows: after an initial display of discomfort they lose lateral stability and swimming co-ordination, tending to swim head downwards; they dart spasmodically and sometimes violently around before sinking helplessly to the bottom, where they may twitch occasionally for some time.

Reports of fish mortality in nature due to high temperature appear to be rare. Huntsman (1946) described extensive mortality of several species in Canadian streams attributable to high temperatures, his interpretation being supported on

experimental grounds by Fry, Hart & Walker (1946). Lake (1957) showed that the same sort of mortality may occur in trout streams in New South Wales. It is most likely to happen when high temperatures are encountered on several successive days when, even if one exposure is insufficient to kill the fish, the phenomenon of summation may result in a lethal exposure. Of course, upper lethal temperatures are more likely to be encountered where fish have little chance of escaping from affected areas. Thus D'Ancona (1954) stated that summer heating of brackish water lagoons in Italy may be lethal to fish when oxygen is low. Indeed, lethal temperatures have been measured for the tench because of the need to know whether they are ever likely to be exposed to dangerously high temperatures in the farm dams in which they have been used in fish cultural experiments (Weatherley 1958). It is safe to state from the evidence shown in Fig. 1 and from recorded maxima in farm dams in Tasmania that temperatures in dams would never be high enough to affect tench adversely.

(*b*) *Survival in high concentrations of carbon dioxide*

The Water Pollution Research Laboratory (Southgate 1956, 1957) showed that approximately 0·4 p.p.m. oxygen was the lowest concentration tench could survive at 16° C and in this respect they were easily the most physiologically robust of nine fish species tested, thus confirming popular notions of their respiratory tenacity. But there appears to be no information regarding their tolerance of higher concentrations of carbon dioxide, and knowledge of this is needed if a reasonably complete picture of respiratory tolerances of tench is to be formed.

Tench were exposed to high concentrations of carbon dioxide in combination with low concentrations of oxygen by placing them in live-boxes in a plant-filled farm dam, one box at the surface and the other at the bottom. At the bottom, carbon dioxide values over 24 h ranged from 20 to 43 p.p.m. (mean 33 p.p.m.), while oxygen remained close to a mean of 1·7 p.p.m. At the surface, carbon dioxide values were somewhat lower and oxygen higher. All tench survived, though they showed distinct discomfort in the bottom live-box. They were left in the dam for 11 days, during which only one tench (in the bottom box) died.

In contrast to this tolerance Alabaster, Herbert & Hemens (1957) showed that rainbow trout died within a few hours under quite similar conditions to the above; temperatures in their experiments ranged from 12·5 to 19·5° C, while those in the farm dam remained close to means of 15·9° C (surface) and 14·9° C (bottom).

(*c*) *Salinity tolerance*

Laboratory experiments in glass tanks showed that though a salinity of 15·4‰ (obtained by dilution of sea water) was fatal within 24 h to tench taken straight from fresh water, they were just able to survive at a salinity of 13·8‰ though it completely disabled them. Chlorinity was estimated by the usual method of titration with silver nitrate solution, salinity then being obtained from Knudsen's (1901) tables.

Further experiments were performed in a metal tank 1·2 m square and 0·6 m deep, painted inside with chemically inert plastic. The earlier experiments were generally confirmed, though it was learned that 24 h is not long enough for reliable indication of deleterious effects at critical salinity levels. Fig. 2 depicts the final experiment in which eight tench were exposed initially to a salinity of 10·75‰. The fish survived for 37 days before showing impairment, while evaporation caused salinity to increase to 14·58‰ as the figure shows. The highest salinity tench could tolerate for 24 h without apparent harm, when they were exposed directly without prior acclimatization, is also marked. To avoid pollution they were not fed during the test, and this probably influenced their performance, if at all, unfavourably.

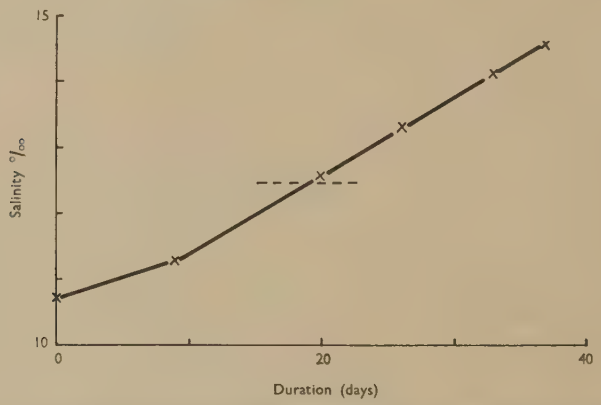

Fig. 2. Effect of acclimatization on survival in higher salinities. Increase in salinity through evaporation is shown. The highest point on the curve represents the salinity where the first signs of disablement of the fish were noted. The broken horizontal line shows approximately the maximum salinity tench were able to survive without prior acclimatization.

Tench have been reported to the writer as living in the River Derwent Estuary at a place where Guiler (1955) reported surface salinities of 3·8‰ (summer ebb tide) and 9·96‰ (winter flood tide). They could presumably live indefinitely in such salinities, though there is no other information on their occurrence in brackish water in Tasmania. However, they form part of the Finnish commercial fishery in the Baltic Sea (Siltamaa 1956) where the coastal salinities appear to be about 5 to 6‰.

FOOD

In common with other Cyprinidae tench lack jaw teeth but possess pharyngeal teeth. These teeth apparently break the food up after ingestion, though many of the smaller food organisms reach the 'stomach' undamaged. The 'stomach' is a simple, rather more muscular expansion of the alimentary canal, evidently having as its chief task the mixing of the food. It does not seem to grind or crush much, nor to play much part in the digestion of the food, since many of the food organisms are still recognizable even when they have reached the anterior part of the intestine.

While it is not intended to discuss tench 'stomach' function here, it may be observed in passing that according to some views most Cyprinidae do not possess physiologically functional, or histologically differentiated, stomachs at all. The pharyngeal teeth, instead of the stomach, apparently serve to macerate the food (Barrington 1957).

While it has sometimes been asserted that tench eat plants Schaeperclaus (1933), in one of the most authoritative statements on the subject, reported that their food habits in ponds overlapped those of the common carp; *i.e.* they ate mainly molluscs and insects. To discover something of the food habits of Tasmanian tench 216 were examined, of which 141 came from Lake Tiberias, 57 from farm dams and 18 from a hatchery pond.

(*a*) *Items consumed*

Table 1 shows the identifiable food items in the guts of Lake Tiberias tench from 2·3 to 20 cm long. Though algae appeared in the gut contents of all the size-groups they were quantitatively unimportant, apparently having been ingested accident-

Table 1. *Gut contents of tench from Lake Tiberias*

The values given are the percentages of the total number of fish in each size-group which contained the item.

	Fish length-groups (cm)							
	2·3-3·0	3·1-4·0	4·1-5·0	5·1-6·0	6·1-8·0	8·1-10·0	10·1-20·0	20+
Number of fish	34	35	25	10	14	12	10	2
Food item								
Copepoda	85	83	64	70	86	42	40	50
Cladocera	94	86	80	70	86	75	70	0
Amphipoda	44	74	88	90	79	42	60	50
Ostracoda	0	6	28	40	29	33	40	50
Chironomidae	26	37	36	20	50	33	30	50
Odonata	0	0	0	0	7	42	50	100
Ephemeroptera	0	0	0	0	14	50	60	0
Hemiptera	0	0	0	0	2	8	10	0
Hydracarina	9	23	0	20	14	8	10	0
Oligochaeta	0	0	0	10	21	0	0	0
Mollusca	0	0	0	0	7	8	10	50
Algae	68	46	48	50	50	25	30	0

ally with actual food organisms. Small crustaceans—Copepoda, Cladocera, Amphipoda, and to a lesser extent Ostracoda—occurred frequently. These were the most important food to fish below a length of 6 cm, though some small Chironomidae were also taken, and a smaller number of Hydracarina. Among larger fish aquatic insects, principally Ephemeroptera and Odonata, comprised by far the major part of the food, though Chironomidae were most numerous. In the larger fish Hemiptera and Mollusca were also found. Hydracarina appeared in small quantities, but without much relation to fish size, and Oligochaeta were present in a few fish.

Twenty-six fish from 11·7 to 20·2 cm long, collected from a farm dam, were

examined. Pulmonate molluscs were their most important food, occurring in at least eighteen gut contents. Lamellibranchs were also found, with scant occurrences of Coleoptera, Odonata, Chironomidae, Trichoptera, Copepoda and Amphipoda. About the time of this fish collection Gastropoda and Lamellibranchia were the most abundant animals of the bottom fauna in the dam, both as to weight and number. Small Oligochaeta were also present but they did not appear in the food and no reason for this can be suggested. However, in another dam Oligochaeta were the most important food among fish whose length ranged from 21·3 to 24·6 cm with Chironomidae next. In a third dam Chironomidae were easily the most important food, occurring plentifully in every gut of seventeen fish from 20·0 to

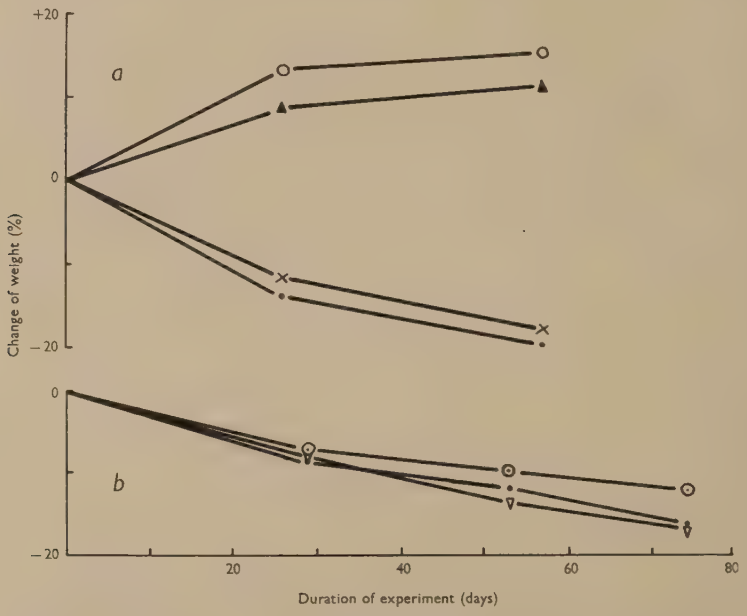

Fig. 3. Changes in weight of tench during the feeding experiments described in the text: *a*, experiment 1; *b*, experiment 2. Foods: ×, *Ranunculus*; ○, liver; ▲, *Ranunculus* and liver; ▽, sedge; ⊙, Myriophyllum; ●, no food (control).

31·7 cm long; Coleoptera, Odonata, Trichoptera and Ostracoda also occurred, though in unimportant amounts, and most guts contained mud, presumably reflecting the way in which tench ingest their food. Bottom faunas of these latter two dams were not examined.

Among tench which had been held in a small hatchery pond for some months many algae were found in the gut contents. Considerable quantities of *Oedogonium* spp. were found in most, *Tabellaria* spp., Gomphonemataceae and Desmidaceae following, in that order of importance. Insignificant amounts of other algae were also found. In addition, half the fish had eaten the higher plant *Potamogeton* sp., of which there was much in the pond, and from which they had evidently sucked

its abundant epiphytic algae in their search for animal food in very overcrowded conditions.

(*b*) *Feeding experiments*

Two experiments were carried out in summer in small hatchery boxes supplied with running water. Dimensions of the boxes were 60 × 40 cm and water was maintained at a depth of 15 cm. In the first experiment three groups of four fish were offered two potential foods, two of the groups each receiving one of the foods, the third group receiving both; a fourth group received no food, thus serving as a control. The foods were ground cooked ox liver and the higher aquatic plant *Ranunculus trichophyllus*. A small amount of natural food may have entered each box with its food supply, but this would have been equal for all boxes and has been ignored. Fig. 3 shows that those fish offered plant lost weight at a rate similar to the control group, but the groups receiving liver alone, and liver in addition to plant, both gained weight at similar rates.

In the second experiment one group was offered *Myriophyllum elatinoides* and a second group a sedge (probably *Schoenus fluitans*, but not of certain identity because flowers and fruit were missing), a third control group again receiving nothing. As Fig. 3*b* shows the groups offered plant again lost weight at rates similar to the control.

AGE DETERMINATION AND GROWTH-RATE

(*a*) *Description of scales and recognition of annuli*

Scales were removed from an area anterior to the dorsal fin and mid-way between the dorsal mid-line and lateral line. Tench scales are thin, flexible and fairly tough; they are easily removed, even though rather deeply embedded, except from very large fish. The upper surface of a scale is dissected by radiating grooves (radii); primary radii diverge from the nucleus, secondary radii appearing further out as the scale grows. The scale is also covered by closely spaced circuli, which tend to encircle the nucleus, though they are often incomplete and run together, especially on the anterior sector of the scale. The circuli are by far clearest on the posterior part and sides of the scale, and it is here that breaks or annuli attributed to cessation of growth in winter were detected. Circuli are continually being formed during growth, being laid down first on the posterior edge of the scale. Progressively more complete circuli are thus found as the more anterior aspects of a scale are examined. It appears that the first circuli formed in spring, on resumption of growth after a winter cessation, completely surround those still incomplete at the scale edge, thus forming a break or annulus. Evidence of the validity of the use of these breaks in estimating age will be adduced below.

The scales of small tench are approximately circular with a nucleus located eccentrically, nearer the anterior than the posterior edge, but as the scales grow they elongate antero-posteriorly more rapidly than in other directions. The eccentricity of the position of the nucleus thus becomes exaggerated, and the final

shape assumed by a scale is that of an oval with rather straight sides, somewhat broader posteriorly than anteriorly.

(*b*) *Breaks* (*annuli*) *as age indicators*

Tench have been observed in hatchery troughs provided with a layer of mud. Here they buried themselves in winter, remaining in a torpid condition. This corresponds to European observations on the species (Yarrell 1841, Lunel 1874), and it seems likely that this period of inactivity would leave its mark on scales.

Many small tench were captured in Lake Tiberias in 1954 and some were released in two farm dams (Weatherley 1958). Survivors of this release, captured and examined 8 months later, before passing their first winter in the dams, bore two breaks on their scales. A broad band of circuli surrounded these, extending to the scale margin. The fish were again released and passed a total of two winters in the dams, which were clearly marked on their scales by corresponding breaks. Finally, then, there were two relatively closely spaced breaks reflecting growth typical of Lake Tiberias and signifying winters passed in the lake, while a broad

Table 2. *Lengths of tench at capture*

	Age at capture								
	1+	2+	3+	4+	5+	6+	7+	8+	9+
Coal River									
Number of fish	–	2	24	52	59	76	34	10	6
Mean length (cm)	–	7·0	11·5	16·3	20·5	23·3	25·7	29·1	29·6
Lake Tiberias									
Number of fish	26	34	51	75	52	15	2	3	
Mean length (cm)	3·9	6·9	9·3	11·5	13·4	14·8	20·7	26·5	

zone of circuli separated the third break from the second, with a rather narrower zone between the third and the fourth breaks. This experiment clearly demonstrated that scales could reveal the number of winters through which tench lived. It may be noted that growth in the dams was much more rapid than in nature (Fig. 5); for an explanation of the possible significance of this see Weatherley (1958). Table 2 gives mean lengths at capture of the various age-groups from the Coal River and Lake Tiberias. 'Growth' curves drawn from these data would, of course, lie above growth curves drawn from back-calculated length-for-age.

(*c*) *Back-calculation of lengths*

If breaks may be accepted as annuli, as shown above, then successful back-calculation of length-for-age depends merely on knowing the relation between increase in length of fish and scales. To this end three scales were taken at random from the sample which had been collected from each fish and in Fig. 4 their mean lengths have been plotted against total fish lengths. To measure them, their images were projected on a screen by means of the apparatus described by Nicholls (1957), and these images were measured from the nucleus along the antero-posterior

axis by means of a graduated rule, which itself was merely a reproduction of an image of a microscope slide scale, graduated in fractions of a centimetre and magnified to the same extent as the fish scales. Direct measurements of the scales in fractions of a centimetre were thus possible.

The relation between scale lengths and fish lengths is rectilinear and the regression line for the Coal River fish intercepts the x axis very close to zero, actually at a negative value, which may safely be ignored since it is so small. Although the regression line for Lake Tiberias fish intercepts the axis 1·7 cm from zero this has also been ignored, back-calculations being carried out as if it also passed through zero. The main reason for this decision is as follows: From 1953 to 1956 several

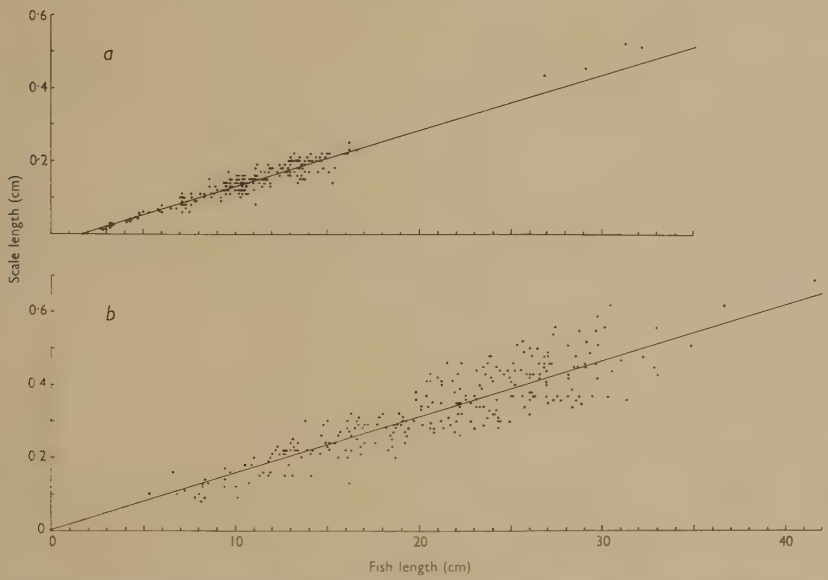

Fig. 4. Regressions of scale length on fish length for: *a*, Lake Tiberias tench; *b*, Coal River tench.

collections of tench were made from Lake Tiberias. These contained, especially in the spring, many fish about 3 cm or even less in length. These were fish which had been spawned the previous summer and just passed their first winter in the lake, as could be seen from their scales. Yet if the positive intercept of the x axis were taken into consideration in back-calculating length then early growth of tench would appear greater than in Table 3. L_1 in particular would be about 4 cm, which is shown as unlikely in view of field observations, though later lengths-for-age would not be significantly changed from those shown in Table 3. Additional support for the view adopted here is afforded by the demonstration by Nicholls (1957) that the scale-fish regressions for different batches of brown trout displayed both positive and negative interceptions. He concluded that 'the significance of

this would appear to be that regression lines based only on small samples are likely to be only approximate'.

(d) Growth-rate of fish from back-calculated length-for-age

Since breaks on scales may be taken as indicators of winters passed and direct and simple proportionality was assumed in practice between fish and scale lengths, calculation of length-for-age was quite simple. Data obtained from scales of 263 fish from the Coal River indicated growth which was steady but not very rapid (Table 3). Apparently higher growth-rate than normal in the 1944-5 year-class may be disregarded, because of the small number of fish involved. There seems otherwise to have been a small but regular increase in growth-rate of the population.

Table 3. *Back-calculation of length-for-age (cm) from scale reading*

Year-class	Number of fish	Age (winters) 1	2	3	4	5	6	7	8
Coal River									
1944-5	9	2·6	5·2	8·8	12·9	16·8	21·0	25·1	27·7
1945-6	27	2·8	5·1	8·5	12·0	15·9	19·9	22·8	24·4
1946-7	56	3·0	5·4	8·7	13·4	18·0	21·4	23·8	
1947-8	71	3·0	5·8	9·7	13·7	18·0	21·0		
1948-9	42	3·1	6·1	10·3	14·2	17·2			
1949-50	43	3·1	6·1	9·9	13·1				
1950-1	13	2·9	6·0	9·0					
Lake Tiberias									
1947-8	15	2·6	4·8	6·6	9·2	11·6	13·4		
1948-9	54	2·7	4·8	7·2	9·7	11·9			
1949-50	73	3·0	5·3	8·0	10·2				
1950-1	43	2·9	5·4	7·9					
1951-2	29	3·0	5·4	7·3					
1952-3	6	3·3	5·7						
1953-4	9	3·2	4·6						
1954-5	24	2·8							

Data from the scales of 257 Lake Tiberias tench revealed a growth-rate more uniform between year-classes and slower than for Coal River fish. The type of growth was similar, however, again featuring small but regular increments. A few tench from the Clyde, Macquarie and Meander Rivers were also examined. The data obtained from their scales are too scanty to include here, but their mean growth-rate fell somewhere between those of the two populations described above. In farm dams tench were able to grow much more rapidly than has been observed in wild populations (Fig. 5), as has been shown elsewhere (Weatherley 1958).

Schaeperclaus (1933) stated that female tench grow considerably faster than males. No significant difference (t test) was detected between males and females from the Coal River. There was a difference (1% level of significance) between the sexes at L_4 for Lake Tiberias; otherwise in this population too the growth-rates were similar. Data from both sexes have been pooled in the above presentations. Despite clear differences in form often apparent between larger males and females

(Andrès 1897), fish less than 10-12 cm long could not be sexed reliably on external appearance. In this investigation tench were sexed only if they were 'ripe' or very large, and therefore of obvious sex, or if they could be dissected.

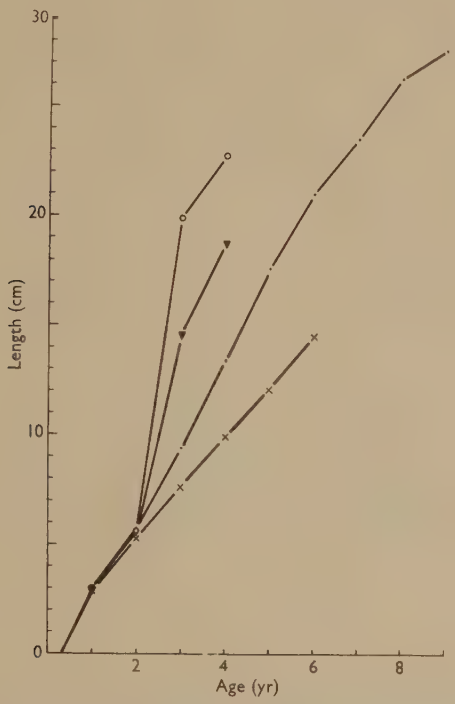

Fig. 5. Mean growth (all year-classes combined) of Coal River and Lake Tiberias tench compared with the growth of tench from experimental dams 1 and 2. ●, Coal River; ×, Lake Tiberias; O, Dam 1; ▼, Dam 2.

CONDITION

Condition (K) was calculated from the formula

$$K = \frac{W10^2}{L^3}$$

following Carlander (1950). Several collections from the lake showed a considerable range in condition to be normal, at a given moment, for fish of similar length. Moreover, condition generally increased with fish length up to 15 cm or more. Fig. 6 demonstrates both these points. In Fig. 7 greatest depth and greatest breadth are plotted against length of the same fish. At least over the range 5 to 15 cm fish length, depth and breadth are linearly related to length, so for this range allometric growth cannot be the cause of the increase in condition.

The number of fish captured in the Coal River at any one time was insufficient

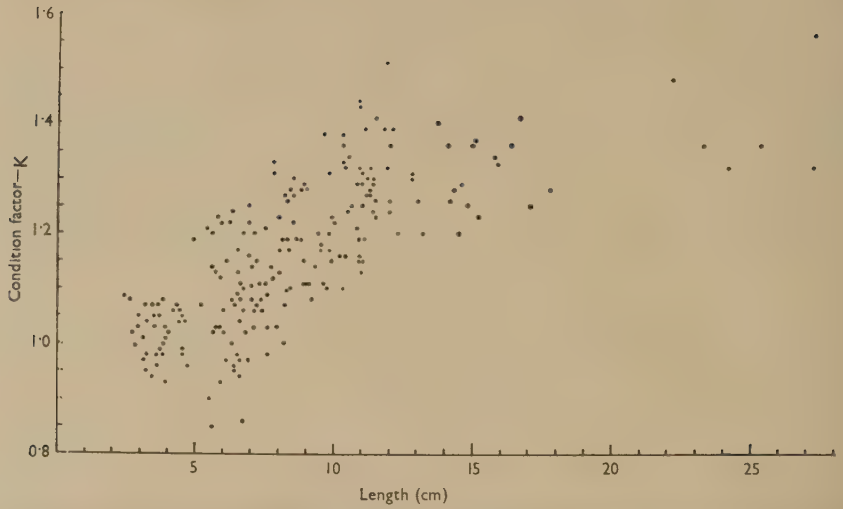

Fig. 6. The relation between condition factor, *K*, and length for tench captured in Lake Tiberias on 12 September 1956.

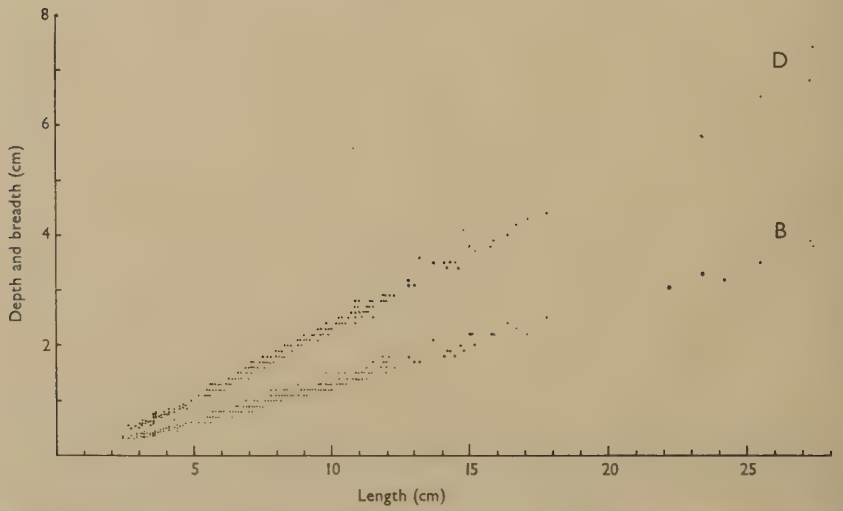

Fig. 7. The relations of greatest depth (D) and greatest breadth (B) to length for tench captured in Lake Tiberias on 12 September 1956.

to determine the relation between condition and length in this environment. But sufficient larger fish were obtained to show that condition fluctuates seasonally. Condition factors, K, for fish 20 to 30 cm long are plotted against dates of capture in Fig. 8.

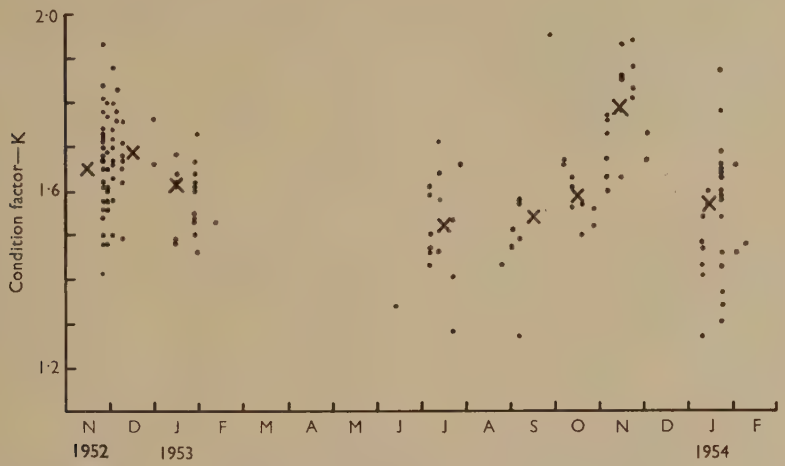

Fig. 8. Condition factor, K, throughout the year for Coal River tench 20-30 cm long. Crosses show the mean values of K for those months during which at least five fish were captured.

DISCUSSION

Tench are very tolerant to low concentrations of oxygen and high concentrations of carbon dioxide, and also to high temperatures, to which their tolerance varies according to the season. They commonly occur in meanders of rivers but could also exist in swamps, weedy fish ponds and waters which were heavily polluted with organic materials. Rosa's (1958) statement that tench can live comfortably between 15 and 32° C has been generally confirmed in this investigation, though he does not discuss the important function of acclimatization in limiting upper lethal temperatures. It is improbable that distribution of tench in nature would be much limited by high temperature, except perhaps in the egg stage, where it might be crucial. But even this seems unlikely, for though Rosa (1958) stated that in their area of natural distribution tench avoid extremes of cold or warmth, he also pointed out that they can survive transplantation to countries as close to the equator as Indonesia.

Tench tend to aggregate in deep holes and shade and are generally sluggish in temperate climates. This 'cryptic' behaviour, coupled with a lack of migratory movements and inability to live in water even of half the salinity of the sea, makes it appear likely that the original distribution of tench in Europe would have been rather limited. Their present wide occurrence there and elsewhere is probably due principally to the agency of man. Even within one river system their distribution

is patchy, partly because of their sedentary disposition and probably partly because of their habit of depositing their eggs among weeds, which do not occur along the whole course of many rivers.

Tench growth-rates range from slow (Lake Tiberias) to quite rapid as in farm dams (Weatherley 1958, Rosa 1958). Their habit of eating various invertebrates makes it seem improbable that they need special groups of organisms (or specially large organisms) for high rate of growth, but rather that quantity of food available, fish population density, and other factors such as light and temperature, will govern growth. Despite repeated statements, some of which are quite recent (*e.g.* Schindler 1957), tench appear to be unable to utilize plants directly as food.

Condition factor, K, as calculated here is related both to length and sexual condition and should not be considered without reference to them, while at any time variation in condition for a particular size-group is considerable. It thus becomes difficult to compare the K value of 1·3 (calculated in the same way as in the present paper) given by Schaeperclaus (1933) as normal for tench in fish ponds, with the Tasmanian values for wild populations and in farm dams (Weatherley 1958). He does not discuss the effects of the factors mentioned above in modifying condition except in stating that there may be 'small differences' ascribable to amount of food in gut, or gonad development.

Seasonal changes in condition in tench, as exemplified by the Coal River population, resemble those in the perch (Le Cren 1951) but with certain differences. Fig. 8 shows that condition rose from a mean low of about 1·5 to a mean maximum of about 1·7-1·8 in midsummer, with a subsequent decline corresponding to time of spawning. This cycle is simpler than for the perch which spawns in spring; perch thus have time during the summer to reach a second peak of condition, before declining to a winter minimum. But both species share in common changes in condition referable to periods of maximal and minimal growth, and spawning time.

ACKNOWLEDGMENTS

The author wishes to thank Mr G. T. Boss-Walker of Ouse, Tasmania, who made dams on his property available for growth-rate studies of tench; the Salmon and Freshwater Fisheries Commissioners for making available facilities in their Plenty River Hatchery, and for permission to trap tench; Mr K. A. Pyefinch, Director of the Freshwater Fisheries Laboratory, Pitlochry, Scotland, and Mr H. C. Gilson, Director of the Laboratory of the Freshwater Biological Association, England, for gifts of tench.

SUMMARY

1. Introduced into Tasmania in the nineteenth century from the British Isles, the tench occurs there, as in Europe, in still or slow-moving, weedy waters.

2. Lethal temperatures are greatly influenced by seasonal differences in acclimatization; tench captured in summer have much more heat tolerance than those taken

in the winter. Tench have high respiratory tolerances which permit them to survive in environments from which other fish would be excluded. Their salinity tolerance is unremarkable, but they apparently sometimes pass a normal life in brackish water.

3. Tench are generalized invertebrate feeders, tending perhaps to increase the average size of the food organisms ingested as they grow.

4. Growth-rate may be slow or fairly rapid, depending on environmental factors. Condition, K, is influenced by size and, among the larger fish, time of year; thus it is highest in summer before spawning and lowest in winter, the time of minimal growth and activity.

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THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* FORSKÅL) IN THE ISLAND OF SOCOTRA

By G. POPOV

*Desert Locust Survey, Nairobi**

(With Plate 2 and 3 Figures in the Text)

The position of the island of Socotra, on the possible migration routes of desert locust swarms between Arabia and the Somali Horn of Africa (Fig. 1), makes records of the occurrence of the locust there of special interest. The reports of

Fig. 1. Position of Socotra in relation to adjacent countries.

desert locust breeding on the island in the winter of 1952-3 induced the Desert Locust Survey to send the author to carry out control operations and to make a general survey of the island from the point of view of its suitability for the desert locust. The visit was from January to April 1953. The following account incorporates observations made during the visit and such previous records as could be found at the Anti-Locust Research Centre in London. The author wishes to acknowledge his gratitude to Dr R. C. Rainey for his assistance with the analysis of swarm movements.

Knowledge of the past history of the desert locust in Socotra is very scanty. As

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the island is rarely visited, it is not surprising that there were no reports of swarms or hoppers there until 1942, when an outbreak of hoppers was reported, though without details, to the Department of Agriculture at Aden on 21 December. After 1942 Socotra presumably remained clear of swarming locusts at least until December 1945, for until that year a Royal Air Force detachment was stationed there, and any large scale infestation could hardly have escaped notice. The next known breeding occurred in the winter of 1950-1. This information was obtained during the present writer's visit. Memories were by then a little vague and the only details obtainable were that the infestation was largely confined to the western end of the island and that egg-laying followed rains, which fell at about the same time as in the winter of 1952-3 (November-December). Some of the local people consulted remembered having seen pink locusts (*i.e.* young adults) about 2 months later, in February, but their fate was unknown.

In early June 1952 a ship reported dead locusts floating on the sea off the northern coast of Socotra over a distance of 5 miles. This does not necessarily mean that the locusts originated on the island; the natives were quite unanimous in their affirmation that no egg-laying by locusts took place there during the period between 1950-1 and 1952-3, although some remembered having seen pink adults in 1952, at the beginning of the 'kharif' (monsoon) season (normally the first half of June), and these disappeared soon afterwards. This brings us to the 1952-3 breeding. The initial arrival of swarms and the oviposition which, according to native sources, followed soon after, were not observed by the writer, but judging from the fact that the hopper bands seen on 25 January 1953 in the vicinity of Hadibo contained all instars from the first to the fifth, egg-laying in this locality probably occurred between early December and mid-January. At Kalansiya, where fledging first took place a week earlier than at Hadibo, the first laying must also have occurred that much earlier, *i.e.* in late November. Eggs were laid over most of the island, mainly on the coastal plains but also in the highlands, wherever soft soil occurred, sometimes in minute pockets in rock crevices. The only area in which apparently no laying occurred was the western part of the limestone plateau, where no hopper bands were reported. Moisture conditions essential for the successful oviposition were ensured by frequent rains throughout November, December and January. Some showers were also recorded in February and the vegetation was lush and green, particularly in comparison with that of the coastal areas of the mainlands.

Considering the size of the island (70×20 miles), the resultant infestation was very heavy. Few areas were clear of hopper bands, particularly when the hoppers became older and more mobile and the bands increased in size. The majority of bands were small, but some had a front of up to 2 miles. Hoppers were active most of the day with hardly any sheltering or roosting at midday. Morning and afternoon basking seldom lasted for more than 2 hours. Canalization of marching along dry drainage channels was a common feature and the predominant direction of marching was upstream, so that gradually the majority of the bands moved up from the coastal plains into the highlands.

A swarm of the desert locust in Socotra, seen as a misty cloud near the top of Jebel Shehaly, the highest peak of the Haggher Mountains.

(*Facing page 91*)

The first fledging was recorded at Kalansiya on 20 February, and was complete throughout the island by the first week in March. The survivors from control operations continued to move into the Hagghier highlands, where eventually a single swarm of about 6-10 sq. miles was formed. This swarm was first observed at 1400 h on 18 March, when it was seen as a smoke-like cloud against the higher slopes of Jebel Shehaly (4500 ft), the highest peak in Socotra (Pl. 2). It is estimated that the swarm was then 2-3 miles away and at a height of about 4000 ft, or 1000 ft above the point of observation near the watershed at Adho Demalu. It gradually drifted down the slope and by sunset (1800 h), when the air-temperature was 67° F and the humidity 75%, locusts came flying down the light southerly breeze to settle for the night on the watershed in the vicinity of the camp.

Table 1. *Behaviour of the locust swarm at the roosting site at Adho Dimelu on the morning of 19 March 1953*

Time	Temperature (°F)		R.H.	Wind	Cloud	Behaviour
	Dry	Wet	(%)	Direction*		
06·00	61	59	88	S	Clear	Roosting
07·30	72	68	80	Variable	,,	Descending from roosts and basking
07·45	74	72	90	,,	,,	Surging and milling
08·00						As above, some settling and beginning to feed
08·10	75	69	72	S	,,	Feeding actively, but milling continued
09·00	78	70	66	,,	,,	Mass feeding, but some milling
09·30	78	70	66	,,	,,	Feeding less actively, most locusts basking, some milling
10·40	80	72	66	,,	Cu trace	Slight feeding; surging in groups, milling cloud beginning to rise
11·00	80	70	59	,,	,,	Milling cloud increasing in volume, rising further and beginning to drift north
11·10						Take-off continuing, about half of the locusts now on the wing, swarm drifting to north
11·45	82	72	60	S	Cu $\frac{1}{8}$	Swarm continuing to rise and drifting north; disappearing over brow of hill

* Strength slight at all observations.

The following morning, 19 March, observations were resumed (Table 1). It will be seen that the swarm followed a more or less regular pattern of behaviour as described by Gunn *et al.* (1948) and Waloff & Rainey (1951) for swarms of the desert locust under comparable environmental conditions. Local inhabitants stated that the swarm had been in the vicinity for at least a week and that during this period there were regular daily flights similar to that described above.

The swarm apparently left Socotra soon after this, since no information on it was obtained after 23 March. With the prevailing north-east monsoon the direction of displacement can be expected to have been towards the Somali Horn, where an immature swarm was reported from Buran on 28 March. From the weather information (Fig. 2) recorded by ships in and near the Gulf of Aden during this period (and kindly supplied by the Meterological Office, London) it can be seen that the temperatures were at all times above the threshold of 73·5-77° F (23-25° C) required for sustained flight (Gunn *et al.* 1948, Waloff &

Rainey 1951), while the winds were consistently from the north-east and usually above the flying speed of the locusts (11 m.p.h.; *cf.* Gunn *et al.* 1948, Waloff & Rainey 1951, Kennedy 1951), largely excluding the possibility of displacement outside the south-west quarter. Furthermore, the Somali swarm first reported on 28 March not only agreed with the Socotran swarm in size and degree of maturation, but also was the only one to be reported on the Somali peninsula (east of the 43° E meridian) since 18 February. The identity of this swarm appears to have remained recognizable for nearly a month, during which period there were repeated reports from a number of localities in the Erigavo highlands, but it finally became confused with that of swarms invading the Somaliland Protectorate from Ethiopia in late April and early May. A similar movement of a swarm

Fig. 2. Weather observations by ships over the period in March 1953 between the disappearance of the swarm in Socotra and the appearance of the first swarm to be reported on the Somali peninsula (symbols as in Fig. 3).

from Socotra to Somaliland appears to have taken place after the breeding on the island in December 1942. An immature swarm appeared in the Erigavo highlands on 18 April 1943, after a period of absence of swarms on the Somali peninsula dating from 10 March.

While locusts were in Socotra, some predation by many species of birds was observed, particularly kestrels and the resident species of glossy starling. Lizards, scorpions and centipedes were also recorded taking hoppers, but of much greater effect was the parasitization of young adults by *Sarcophaga tibialis* Macquart (Diptera: Calliphoridae). Large numbers of dead and disabled adult locusts

were picked up from the roosting site of the swarm in the Hagghier mountains on the morning of 19 March and others were scattered thinly over a larger area. On dissection the majority were found to contain up to three maggots, while others without maggots had emergence holes between the head and the pronotum. The parasitization was estimated visually at about 5%. *S. tibialis* Macquart is a widespread species, usually regarded as a scavenger. In Socotra, however, it appears to be a common parasite, since it has been reared in numbers from adults of *Pachysmopoda abbreviata* (Tasch.), a common endemic Tettigoniid, in addition to *Schistocerca*.

Since the 1952-3 breeding, the only information received from Socotra was brought by the Oxford University Expedition which visited the island from August to October 1956. Thirteen sight records of adults of the desert locust were claimed, but confusion with other common species of large Acridids, such as *Anacridium melanorhodon arabafrum* Dirsh and *Cyrtacanthacris tatarica* (L.), is quite likely. Only one specimen of *Schistocerca* was actually captured on 18 August, at Kishen. It is a male of reddish coloration, fairly advanced age (not a fledgling) and the general appearance of *S. gregaria*. No other information was obtained. Thus information on the occurrence of the swarming phase of the desert locust in Socotra includes three cases of breeding during the winters 1942-3, 1950-1 and 1952-3, the appearance of an immature swarm of apparently exotic origin in June 1952, and the record of a few adults (only one examined) of unknown origin between August and October 1956.

A study of the summary charts of the seasonal breeding and migrations of the desert locust prepared by the Anti-Locust Research Centre has created a strong impression that the origin of swarms which arrived and bred in Socotra in the winters 1942-3, 1950-1 and 1952-3 may have been connected with the mass movement of swarms that originated in those years in the Indo-Pakistan area to southern Iran, Oman and southern Arabia, some swarms even reaching the Somali peninsula. The best documented of these movements is that of 1952, when the progressive spreading of swarms as far as the Somali peninsula was not confused by the presence of indigenous populations. The first arrival of swarms was recorded at Jask in southern Iran and on the Batinah coast of Oman on 10 October 1952, and on Masira island during 10-12 October. Swarms reached the wadi Hadhramaut on the 18th and the coast of East Aden Protectorate on the 20th; on the 13th a ship reported large numbers of locusts floating in the sea at 12°12′N 63°30′E, a point about 300 miles due east of Socotra. The second wave of swarms reached Jask on 2 November, Oman during 3-5, the Hadhramaut 2-10, and the Somali peninsula during 12-18 November. Judging from the information available, the arrival of swarms in Socotra occurred about the middle of November with the second wave of migration, at about the same time as in Somalia. On this assumption, the weather information for the period 10-20 November has been plotted in Fig. 3, in a manner similar to that in Fig. 2. Once again the temperatures are found to be suitable for flight and although the winds are more variable, they are predominantly from the north-east and in the vicinity and to the north and east

of Socotra, consistently so. This suggests that the origin of swarms arriving in Socotra was unlikely to have been the nearest point on the Arabian mainland, but was more probably some more easterly area of the Arabian peninsula. It is even possible, on the evidence available, that the swarms that reached Socotra came directly from India, where numerous swarms were present on the Kutch peninsula and elsewhere during this period; this possibility is supported by the occurrence, already mentioned, of locusts on the sea 300 miles east of Socotra on 13 October. While Kutch is some 1200 miles from Socotra, locusts in numbers are known to have travelled a comparable distance into the Atlantic from West Africa (Sélys-Longchamps 1878, Howard 1917). A further argument in favour of this view lies in a statement by Rainey & Waloff (1948) that 'upper wind studies, such as those of Ramanathan and Ramakrishnan (1939), and synoptic experience suggest that the air over the Gulf of Aden during the north-east Monsoon originates usually from north-west India or the Gulf of Oman, and only relatively rarely from the interior of Arabia'. This view also shows very close agreement with that expressed by Moreau (1938) on bird migration over the north-western part of the Indian Ocean. It would appear that in autumn many of the bird migrants, including passerines, fly directly from south-eastern Arabia to eastern Africa, with or without a stop on Socotra, while several long-winged species probably regularly migrate across the Arabian Sea straight from India, 1600 miles, which would be the longest such crossing in the world.

On the other hand, the pink locusts recorded near and in Socotra in June 1952 appear most likely to have belonged to the young swarms that were present in the Somali peninsula at this period, since winds reported around Socotra during the first half of June 1952 were consistently southerly and south-westerly. The origin of the pink individuals on the island in summer 1956 is obscure; during June 1956 a few swarms were reported from Asir, Yemen and Aden in south-western Arabia. By July three swarms and some scattered individuals were reported from the Somaliland Protectorate and some may have reached Socotra. However, the evidence does not exclude the possibility that they may have been of local origin.

With regard to the non-swarming phase of the desert locust in Socotra, no information is available. This species was not represented in any of the earlier collections from the island, but it is an agile insect, not easy to catch and it would be expected to occur principally in the sandier parts of the lowlands, which are poorest in fauna and flora and therefore of least interest to general collectors. A fair statement under the circumstances would be that, even if non-swarming desert locusts were present on the occasions when collectors visited Socotra, they could not have been very common. Two adults with the grey coloration and some feebly developed morphological characteristics of phase *solitaria* were captured on the southern coastal plain of Naukad at the end of March 1953, but these might have been derived as the result of dissociation of their parents from the swarms that were present there in November 1952. Further discussion can be only hypothetical. There is no obvious reason why the solitary phase of the

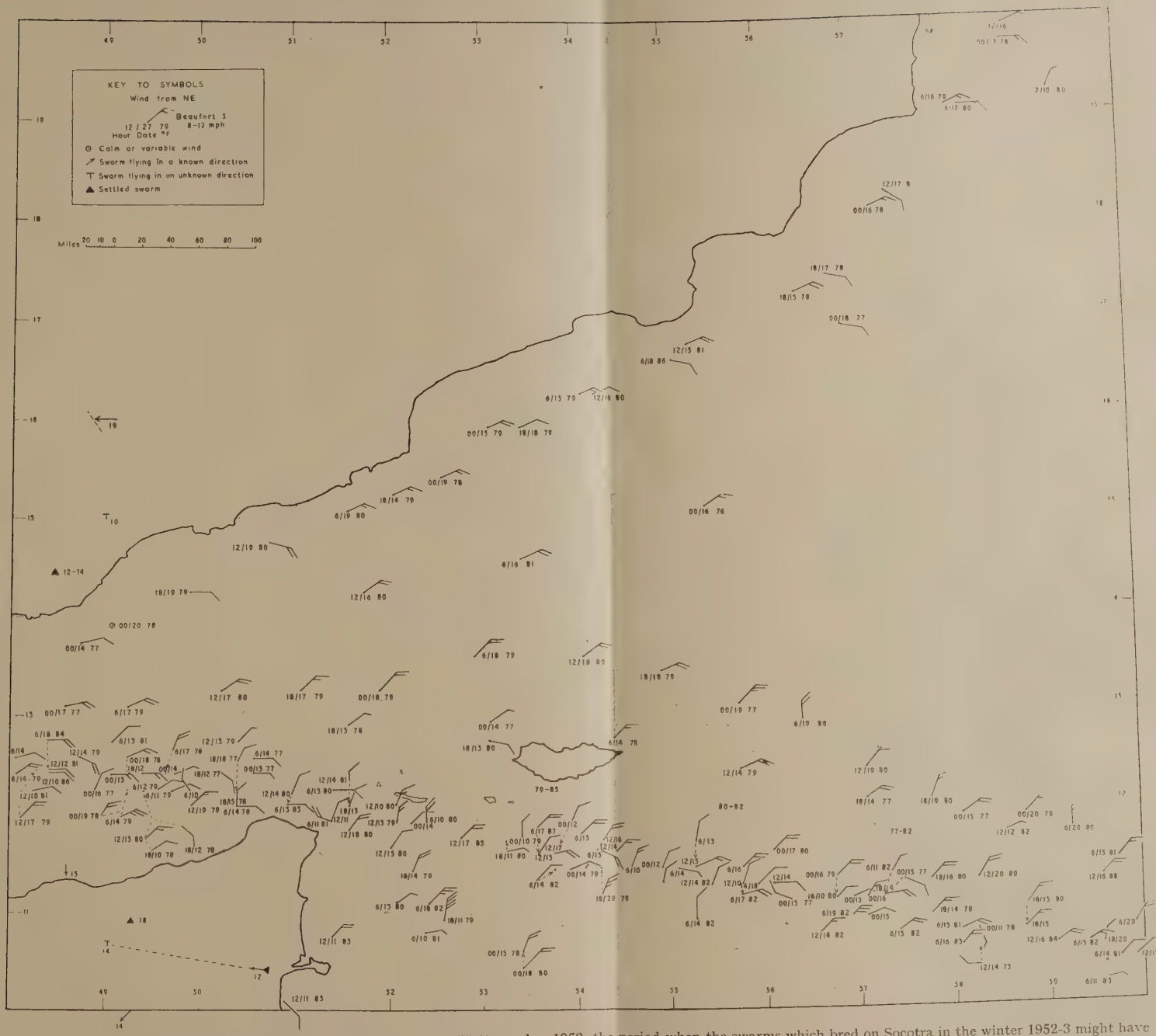
KEY TO SYMBOLS
Wind from NE
Beaufort 3
8–12 mph
12 / 27 79
Hour Date °F
Calm or variable wind
Swarm flying in a known direction
Swarm flying in an unknown direction
Settled swarm
Miles 20 10 0 20 40 60 80 100

Fig. 3. Weather observations by ships during the period 10 to 20 November 1952, the period when the swarms which bred on Socotra in the winter 1952-3 might have reached the island. (The data on swarm movements and weather conditions are indicated by conventional symbols explained in the key.)

(*Facing page 94*)

desert locust should not be able to live in Socotra, since it lives in many parts of the coastal areas of the neighbouring mainlands under similar ecological and climatic conditions.

Assuming that the desert locust does maintain itself in Socotra, is swarming likely ever to arise there and could it contribute to the development of an outbreak? The sandy areas in Socotra are small in extent, even in relation to the size of the island (Popov 1957). The sands are often bare; when vegetation is present, it tends to be uniform. Plants such as *Heliotropium pterocarpum* and *Tribulus* sp. which, in Arabia and on the Red Sea coast of Africa, form matted growths where hoppers become concentrated, are absent from Socotra and not represented by alternative species with similar characteristics likely to act as such concentrating factors. Cultivations of *Pennisetum typhoideum* ('dukhn' of the Arabs), which remain green long after the rest of the vegetation has dried out and thus serve as concentrating factors for adults, do not exist in Socotra, and the few patches of *Eleusine coracana* are too small to be of importance. Concentration in one area of a population built up in another (Rao 1942) also appears unlikely in Socotra. The build-up of the population might perhaps take place in the coastal areas during the winter season, but in view of the uniform nature of *Croton* bush and the bare limestone plateau of most of the island subsequent migrations are more likely to end in dispersal than in concentration, particularly because of the violent 'kharif' winds. Summer rains appear to be rare, and in the absence of irrigated crops and therefore of alternative sites for laying, the production of two generations in a year would be equally rare. It would appear, therefore, that the chances of Socotra being of importance in the dynamics of the desert locust are small, not only by reason of the isolation and relatively small size of the island, but also because of its ecological conditions. However, a visit during a period of recession of desert locust plagues would be necessary in order to find out whether the locust lives there permanently. Well documented records of swarm passage or breeding in Socotra would be of special value for the study of desert locust migrations over the Arabian Sea and the Gulf of Aden.

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THE LIFE CYCLE AND ECOLOGY OF THE FRESHWATER SNAIL *PHYSA FONTINALIS* (L.)

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(With 1 Figure in the Text)

Physa fontinalis (L.) is a freshwater pulmonate which is commonly found amongst the aquatic vegetation in ponds, rivers and streams in Britain and, like other members of the Hygrophila, is hermaphrodite. After leaving the ovotestis, the eggs and sperm pass down the hermaphrodite duct to the point at which the male and female systems separate. The spermatozoa are then carried along the vas deferens and are injected into the copulatory partner by the penis, the foreign sperm being stored in the bursa copulatrix. The eggs are fertilized either by sperm from the same snail, or by foreign sperm moving out of the bursa and up the oviduct. After fertilization, the ova each receive a nutritive covering from the albumen gland and then, as they pass down the female duct, are surrounded by the mucous coats which form the egg capsule. The families included in the Hygrophila exhibit an essentially one-year life cycle with a single breeding season, during which the egg capsules are laid, but, as will be seen below, certain deviations from this annual pattern of reproduction are found.

This paper, which forms part of a series on the reproduction of *P. fontinalis*, describes the life cycle of this species and the fluctuation of the degree of cellular activity in the organs of the genital system has been correlated with this. An analysis of the factors which govern the life cycles of populations in this country has been attempted and comparisons are made with other species. When snails were brought into the laboratory during the breeding periods, many were soon engaged in copulatory activity, and this was followed later by oviposition. The stimuli governing the initiation of these processes were investigated in the hope of obtaining information on the hormonal and nervous regulation of the reproductive behaviour of the snails.

Several studies of the life cycle of pulmonate populations have been made previously; of note are those of Hunter (1953) on *Ancylus fluviatilis* Müller, Brown (1937) on *Physa anatina* Lea, R. M. DeWitt (1954a and b, 1955) and Agersborg (1932) on *Physa gyrina* Say, W. F. DeWitt (1955) on *Physa fontinalis* and Morton (1954) on *Carychium tridentatum* (Risso). These papers are discussed more fully later and many references on copulation, fertilization and oviposition have been collated by Bondesen (1950).

MATERIAL AND METHODS

Specimens of *Physa fontinalis* were collected from a variety of habitats, but observations were made during the period August 1953 to August 1956 at Stanmore

(Middlesex), Lewes Brooks (Sussex), the River Stour (Suffolk) and Windermere (Westmorland). Between March 1954 and May 1955 monthly samples were obtained from a pond at Stanmore. The sampling was random and specimens were taken from all types of vegetation. About 100 individuals were collected in each monthly sample, although the actual total varied around this number, since, to guard against selecting the more conspicuous specimens only, the last collection with the net was always completely emptied. Similarly each separate collection in any one sample was thoroughly checked and every snail removed. When young snails were present in the pond, after the removal of the larger snails in the collection, all the vegetation and plant debris in the net were brought back to the laboratory, where they were placed in large dishes and flooded with water. After a few hours, the young snails crawled to the edge of the dish and so could be easily removed. As a final precaution the vegetation was then thoroughly checked with a hand lens. The shell length of each snail was measured from the apex of the spire to the lip of the peristome and this value represents a standard measurement by which the growth of the colony may be expressed. Larger shells were measured directly to the nearest 0·1 mm, using a micrometer screw gauge, while smaller specimens were placed on damp filter paper and compared with a scaled eye-piece in a low-power microscope.

From each monthly sample, specimens over the whole size-range were dissected and the macroscopic condition of the genital organs examined. Finally, a selection was fixed in Susa, sectioned at 8 μ and stained with Heidenhain's azan or iron haematoxylin. In this way the annual cycles in cellular activity in the genital system were correlated with the variation in shell size of the population throughout the year.

Following the technique recommended by Fraser (1946), small snails and embryos were fixed in Kahle's fluid as well as in Susa, both fixatives giving similar results. Before fixation, embryos were dissected from their capsules in a saline solution, the formula of which is given by Pantin (1948, p. 67) as being isotonic with the blood of *Lymnaea stagnalis* (L.). After embedding, longitudinal sections were cut at 6 μ.

LIFE HISTORY

The vegetation in the pond at Stanmore is largely composed of *Stratiotes aloides* with a marginal zone of *Elodea canadensis* Michx., and on these plants *Physa fontinalis* was found abundantly. Table 1 gives a summary of the results obtained in the monthly collections during 1954-5, showing the range of values of shell size found in any one sample, together with its mean and standard deviation. Although the shells were measured to the nearest 0·1 mm, the lengths were grouped in classes of 0·2 mm and the percentage of individuals in each group was calculated and the results translated into a histogram (Fig. 1).

At Stanmore the main period of reproduction occurs in late spring, during April and May, but generally some of the young snails which hatch from the egg capsules reach maturity by July or August, and a second smaller breeding season

is found. Thus Fig. 1 shows that the snails were reaching their maximum size during April. Specimens collected at this time usually copulated within a few hours, whilst a small number of egg capsules was found in the pond attached to the vegetation, especially *Stratiotes aloides* Linn. Oviposition subsequently became more and more frequent as the snails reached sexual maturity, and during May hundreds of capsules could be found in the pond. At this time almost all specimens oviposited with great regularity when placed in aquaria in the laboratory.

At the conclusion of the first breeding season, the snails die, and the collection on 17 June (Fig. 1) shows that very few of the old individuals remain. Snails collected in May whilst spawning and kept in the laboratory also died about the middle of June. By this time, however (Sample IV), the young snails were hatching, and the most advanced specimens had already reached a size of 6·3 mm. Thus,

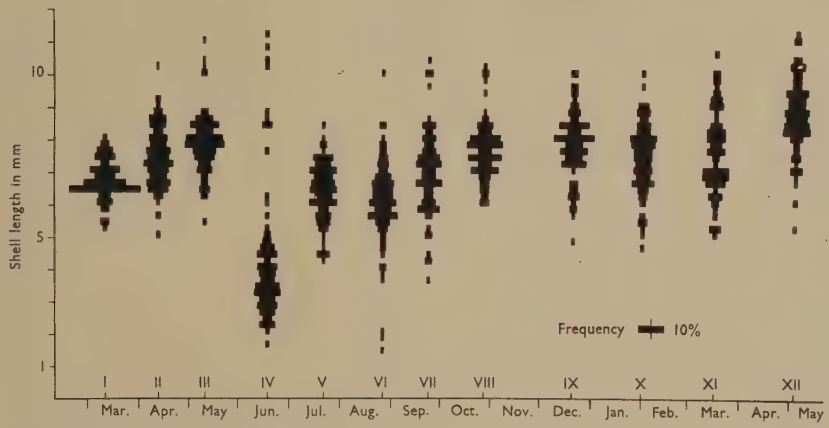

Fig. 1. Histogram showing the percentage distribution of shell length of *Physa fontinalis* in Stanmore Pond during 1954-5. A separate scale is provided to determine the percentage value of each size-group. For further explanation see text.

in Table 1 the collection on 17 June is divided into two lines, *a* and *b*, for the two populations existing at that time.

It can be seen from Table 1 that during the period between March and June, the population as a whole of one-year-old snails, which hatched during the previous year, has been slowly and steadily increasing in shell length as more and more individuals reach their maximum size. The growth-rate of the young specimens which hatch in June, however, is remarkably fast, and it was found that in 1954 many had reached sexual maturity by 21 July, when egg capsules were again found in the pond. In the month between 17 June and 21 July, the mean shell length increased from 3·6 to 6·4 mm.

Egg capsules were found in the pond and were also laid in the laboratory until the last week of August, and the sample taken at that time (Fig. 1) cannot be regarded as a homogeneous population, being composed of both first and second

generation individuals; those around the mean size may be either late or slow-developing members of the first breeding season or advanced specimens of the second generation. However, observations showed that in the summers of 1953 and 1956 a very much smaller percentage of snails reached sexual maturity, and in 1955 no second breeding season occurred. This variation in different years is discussed below.

It is noteworthy that the snails breeding during July and August were all much smaller than those in April and May, and it is evident that they reach sexual maturity before maximum shell size is attained. Apparently the warmer conditions existing in the summer produce rapid metabolic activity and favour or permit copulation and oviposition. After reproduction the animals die, and at this time the giant specimens of late spring, which may be 11 mm, are rarely found. Reproductive activity has ceased by September, and the population is

Table 1. *Shell lengths of* Physa fontinalis *from collections at Stanmore Pond, 1954-5*

	Sample number	Number in sample	Minimum length (mm)	Maximum length (mm)	Mean length (mm)	Standard deviation
1954						
11 March	I	69	5·3	8·2	6·7	0·59
12 April	II	135	5·0	10·3	7·5	0·85
10 May	III	106	5·4	11·0	7·9	0·88
17 June	IV*a*	91	1·7	6·3	3·6	0·93
	IV*b*	9	7·7	11·2	9·4	–
21 July	V	118	4·2	8·5	6·4	0·95
26 August	VI	112	1·5	10·1	6·1	1·3
23 September	VII	83	3·7	10·5	7·1	1·4
27 October	VIII	95	6·0	10·2	7·7	0·84
20 December	IX	95	4·9	10·1	7·8	0·97
1955						
1 February	X	100	4·6	10·0	7·5	1·1
16 March	XI	73	5·1	10·7	7·6	1·3
3 May	XII	92	5·3	11·2	8·8	1·1

then composed of non-breeding individuals derived from both spawnings distributed over a wide size range (3·7 to 10·5 mm). As the season advances the population tends to stabilize itself, the smaller snails maturing and the older individuals probably dying, so that by October the mean shell length is 7·1 mm and throughout the winter there is no significant change in the population structure. Growth then ceases and the maximum, minimum and mean shell lengths remain almost constant until the following spring. With the advent of warmer weather in March growth recommences and the seasonal cycle begins again with the spring breeding period.

GLANDULAR ACTIVITY

As would be expected, there is a variation in the degree of cellular activity and histological development in the reproductive tract of the specimens collected in each sample, and this corresponds with the seasonal fluctuation in size and breeding activity.

The histology of the reproductive system of mature specimens of *Physa fontinalis* has been described elsewhere (Duncan 1958). In April the genital organs are large and active, especially the albumen gland and oviduct. The bursa is filled with its characteristic red pigment, and after copulation the shiny, white mass of sperm can be seen through its transparent walls. All the glandular cells are enormously swollen and stain intensely. The penis is distended, the surrounding sheath of glandular cells is greatly developed and the whole organ is turgid. Both the prostate and albumen glands are fully functional, and after staining with azan the cells of the former appear blue or purple and all the follicles of the latter are lined by cells filled with blue globules. The ovotestis is fully charged with gametes in all stages of development, the majority being mature. The genital system remains functional until the death of the animal, but by late May and June sections reveal a diminution in secretory activity, and many cells are vacuolated. Although the hermaphrodite duct still contains sperm, the ovotestis is almost empty and few gametes remain.

The eggs are laid enclosed in capsules, and under laboratory conditions at 19° C hatching usually occurs about 17 days after oviposition. Observations suggest, however, that in the pond during spring, the young snails emerge in about 4-6 weeks owing to the lower temperatures prevailing at that time of year. The young snail which emerges is in outward appearance a miniature adult, but internally the rudiments only of the reproductive system have been laid down. Fraser (1946) gives a complete account of the development and origins of the genital organs of *Lymnaea stagnalis appressa* Say, and sections of embryos of *Physa fontinalis* which I have dissected from their capsules show that there is a close correlation of developmental sequence between these two snails. In newly emerged *P. fontinalis* the genital system is found to be little more than a strand of cells, but by the time the animals have grown to 3 mm, a small, separate penis has developed. Shortly afterwards the ovotestis differentiates and the reproductive system can be traced as a complete cord of cells from the gonad forwards to the penis. As development proceeds this was found to split longitudinally to give male and female tracts, the former soon becoming functional.

Some of the young snails hatching in June have their developmental history condensed into about 6-7 weeks, so that growth is rapid and the cells of both the male and female systems have reached maturity by the end of this time. In the ovotestis of a normal 6 mm snail there are a few immature ova together with developing spermatozoa in all stages. The latter are mostly spermatogonia and spermatocytes, the majority of the mature sperms filling the hermaphrodite duct. It is significant that the male system, in contrast to the organs of the female tract, is fully functional, the vas deferens having prostate follicles whose cells are in varying stages of secretion. Holm (1946) also noted that in *Lymnaea stagnalis* the male system develops more quickly and reaches maturity before the female tract. Staining with azan reveals the following cycle of events in the oviducts of snails in various stages of secretory activity. The initial red-staining cytoplasm becomes colourless and then takes up the aniline blue. From a homo-

geneous blue coloration, each cell differentiates and becomes divisible into two regions, the nucleus lying approximately at their junction. The basal zone, initially the more extensive, appears as a deeply staining, reticular network, whilst apically the cytoplasm becomes vacuolated and stains less intensely. The apical region then appears to increase in size at the expense of the basal portion, so that the whole cell becomes vacuolated. Although the oviduct is divided into regions with differing functions, the glandular cells throughout follow the same maturation cycle before liberating their secretory products. In the same way, the cells of the albumen gland follow a developmental cycle. Initially, the cytoplasmic contents are granular and stain red with azan, but subsequently the cells give a purple reaction and finally become packed with bright blue globules.

Some of the mature snails resulting from the spring spawning then reproduce and the resulting young snails form the second generation. Hatching takes place in about a fortnight, less than half the time taken for the development of the embryos of the spring spawning. This accelerated development is almost certainly due to the higher temperatures prevailing and compares with the hatching time of capsules maintained at 19° C in the laboratory. In the young snails of this second generation, growth is also rapid, so that by September with a mean shell length of 7·1 mm, the reproductive organs have reached the winter condition. The snails which result from this second breeding season, together with the slower-developing individuals of the spring spawning then overwinter together. In all specimens the ovotestis is large and packed with male gametes in all developmental stages, but none of the ova are mature. The hermaphrodite duct is filled with spermatozoa and the whole of the male system is fully developed. The staining reaction of the prostate follicles and the praeputial gland indicates that they are capable of active secretion, but no copulation occurs throughout the winter and the penis lacks the greatly swollen layer of gland cells so characteristic during periods of reproductive activity.

The female system is in complete contrast, the oviduct being so small as to be almost indistinguishable and appearing in sections as an extremely narrow duct, although in larger snails oviduct II can be seen as a rudimentary evagination. The cells of both the minute albumen gland and the oviduct stain red with azan, indicative of their immaturity, and the whole female tract is enclosed in a fatty sheath. The bursa is rudimentary and does not contain sperm. The genital system remains in this condition until the following March, when the female tract rapidly develops to maturity, although copulation may begin whilst the cells of the oviduct are in a non-secretory condition.

It has been suggested (Duncan, unpublished thesis) that this 'condensed protandric sequence' represents an evolutionary relic of the ancestral condition found in the Ellobiidae, in which the reproductive cycle in certain genera has been described by Morton (1954, 1955a, b). Thus, in *Carychium tridentatum*, the gonad shows a phase of sperm production which is gradually replaced by a phase of ovogenesis. The penis and vas deferens only are present in specimens collected in July and August, during the male phase, and after this the glandular portions of

the female duct gradually increase in size, reaching maximum development in the female phase. During the development of the female organs, the sperms, once liberated from the ovotestis, are stored in the glandular portion of the hermaphrodite duct.

FACTORS INFLUENCING THE LIFE CYCLE

The results recorded above and illustrated in Fig. 1 relate to the population of *Physa fontinalis* in Stanmore Pond from March 1954 to May 1955, but subsequent observations in the same locality during the latter part of 1955 and also in other districts throughout this two-year period indicate that this sequence of events is not typical of every community of *P. fontinalis*. Table 2 sets out the mean monthly air temperatures at Wealdstone, taken from data supplied by the courtesy of the Meteorological Office, Air Ministry, London. Wealdstone is about 2 miles from Stanmore and is the nearest meteorological station for which temperature records are received by the Air Ministry. It is not assumed that these data reflect accurately the temperature of the surroundings in which the snails live; since water has a large heat capacity it seems certain that the temperature of a pond will not exactly follow the air temperatures of its surroundings. However,

Table 2. *Mean monthly air temperatures in °C at Wealdstone, Middlesex, 1953-5*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1953	–	–	–	–	–	–	15·8	17·0	14·1	10·5	7·9	7·3
1954	3·0	3·1	6·3	7·5	11·9	14·3	14·9	15·4	13·4	12·2	7·2	6·3
1955	2·6	1·9	3·7	9·7	10·7	14·9	18·3	18·8	14·1	–	–	–

the mean monthly air temperatures provide a very good indication of the prevailing conditions in which each generation matured.

The records of shell length begin with adult snails in March 1954, so that air temperatures from July 1953 are given, since it was from this time that this population had been maturing. Table 1 shows that the growth of the second generation proceeds in two major phases. Young snails hatching in August grow rapidly and by late September have reached a mean shell length of 7·1 mm. Winter is a quiescent period with little change in shell size or development, and it is not until the spring that growth begins again. However, the young snails hatching in June grow rapidly and continuously, reaching breeding condition in 6-7 weeks. It appears that the most important factor governing the rate of development is temperature, growth being negligible at air temperatures below about 7° C and recommencing once this value is reached in spring.

Factors other than temperature must also affect the growth-rate. The snails in the spring of 1954 bred at a much smaller size than in 1955, and the mean shell length never reached the value recorded in the latter year. The mean values of shell length for 1954 in the months of March and May are 0·9 mm smaller than in the corresponding months in 1955. This is a statistically significant result, the observed difference of mean values in both cases being five times greater than the

standard error of the difference of the means, calculated from the number in the sample and its standard deviation. However, the temperature records of the two years show a close correlation, and it appears that the 1955 generation, with the larger mean shell length, experienced the slightly colder conditions. The mean monthly temperatures in 1954-5 were generally, except in October, about 1° C below those of the preceding year. In both years the times of copulation and oviposition in the spring were approximately the same, although the factors on which the initiation of these processes depend are complex and are discussed later.

Hunter (1953) noted that the size of breeding *Ancylus fluviatilis* in any one locality varied from year to year, and he suggested that variation in mean shell length in this species can be correlated with the total number of hours of sunshine in the previous year during the period when the young snails were developing. *Ancylus* grazes directly on algae growing on stones on the substratum, and there will be a relationship between the available food and the quantity of light falling on the habitat. *Physa* feeds on a variety of detritus, as well as on algae, and light will probably be of lesser importance in influencing growth-rates.

That growth is not governed solely by a simple relationship with temperature is illustrated by observations made during the summer of 1955, when the weather

Table 3. *Samples of* Physa fontinalis *taken August-September 1955*

		Number in sample	Minimum length (mm)	Maximum length (mm)	Mean length (mm)	Standard deviation
Stanmore Pond	13 Aug.	100	3·3	7·9	5·6	1·05
Lewes Brooks	10 Sept.	99	3·4	5·1	4·1	0·39
River Stour	6 Sept.	89	3·4	7·6	4·9	0·81

was exceptionally warm (Table 2). At Stanmore the young snails hatching in June in that year developed slowly and no second period of breeding activity was found later in the summer. After a collection in August of 100 specimens, only three egg capsules were eventually laid in the laboratory and one more was found in the pond after intensive searching. However, dissection proved that almost all the snails were sexually immature, so that in 1955 only a simple, one-year cycle was found, whereas in the two previous years the sequence of reproduction with two generations occurred. In 1956 a small percentage of the snails reached sexual maturity in late August and laid egg capsules, but the majority overwintered and did not breed until the following spring. Collections at Lewes Brooks (Sussex) and in the River Stour (Suffolk) also revealed that in September 1955 no second spawning occurred in these localities. Table 3 sets out the essential statistics derived from the samples taken from these habitats in 1955, all of which have very low values for the mean and maximum shell lengths when compared with corresponding measurements made at Stanmore in the previous year. No egg capsules or recently emerged snails were found, either at Lewes Brooks or in the Stour, although in the latter locality the river was searched along several miles of its length. It is difficult to suggest any reason for this absence of a second

spawning in 1955, but it seems probable that the very hot weather and prolonged drought, which caused many freshwater habitats to dry up partially, produced unfavourable conditions resulting in retarded growth-rate. It proved difficult to maintain cultures of *P. fontinalis* in the laboratory at 23-4° C and the snails died quickly. The temperature in Stanmore Pond and Lewes Brooks frequently exceeded this value during the afternoons in August 1955, and this probably proved unsuitable for normal growth. Snails kept in the laboratory under unfavourable conditions, with restricted food supply, in water polluted by bacterial scums, or in isolation, invariably grow very slowly, but occasionally produce fertile egg capsules, although at a later date than corresponding individuals living in natural habitats or under ideal laboratory conditions.

In the Lake District it seems to be a general rule that only one generation is produced in each year. Samples were taken by dredging in Windermere and shaking the snails from the vegetation so obtained, and also by collecting from the stones in the shallow water at the edge of Loughrigg Tarn. In both habitats,

Table 4. *Samples of* Physa fontinalis *taken from Windermere, 1954-5*

	Sample number	Number in sample	Minimum length (mm)	Maximum length (mm)	Mean length (mm)	Standard deviation
1954						
7 July	I*	20	5·1	8·3	6·3	0·83
20 July	II	60	1·4	4·7	2·8	0·67
1955						
1 February	III	34	3·5	5·6	4·6	0·56
8 March	IV	65	3·6	7·8	5·0	0·69
17 March	V	69	3·8	6·1	4·8	0·53
12 April	VI	19	4·3	7·3	5·7	0·79

* Only adult snails included.

only one period of spawning of *P. fontinalis* was found. Breeding activity in this district occurs a little later in the year, both copulation and oviposition continuing until the first week of July. Snails living as far north as this have a much shorter shell length when mature and growth is less rapid. The results obtained from the samples are set out in Table 4. The young snails hatching in July developed slowly, and regular samples were taken again in the following spring to determine the size of the individuals when breeding began. The first capsules were laid in the laboratory after the collection on 12 April 1955, although in general oviposition in the lake was later than this. The mean and maximum shell lengths recorded at this time were 5·7 and 7·3 mm respectively, values very much below those at Stanmore at the same time (mean 7·5, maximum 10·3 mm, see Table 1). Table 5 gives the mean monthly air and lake temperatures at Windermere during 1953-5, being prepared from data which were supplied by the courtesy of the Freshwater Biological Association. The mean air temperatures are calculated from a continuous series of readings, whereas the values for the lake represent the mean of four weekly readings, made during the day time only. The temperature in

Windermere is given at the surface and at 6 m, the depth at which the population of *P. fontinalis* was found.

The temperature data indicate that during the warmer summer of 1955 conditions in Windermere were comparable to those existing at Stanmore in 1954, whereas in 1953 a second breeding season was found. However, in 1955 temperatures were low in Westmorland until June, and the young snails did not hatch until a much later date than at Stanmore in 1954, so that it is not surprising that a second period of reproductive activity did not occur in the lake.

W. F. DeWit (1955) found that in a ditch in the Botshol polder in the province of Utrecht two generations of snails occurred in each year as a general rule. It appears that all, or the majority, of the members of the spring generation bred and then died. This is in contrast to the results obtained from a study of snails living in southern England, where many individuals do not reach sexual maturity until the following year. Furthermore, as stated above no second breeding season

Table 5. *Mean monthly air and water temperatures (°C) at Windermere, 1953-5*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1953												
Air							14·5	15·1	13·3	9·4	8·3	5·9
Lake, surface							17·7	17·4	14·9	12·6	9·4	8·2
Lake, 6 m							–	–	–	–	–	–
1954												
Air	3·4	1·5	4·9	7·4	11·1	12·6	13·3	13·9	11·4	11·4	6·5	6·3
Lake, surface	6·1	4·3	4·4	7·0	10·2	14·2	15·2	15·1	13·4	11·8	9·2	7·2
Lake, 6 m	6·1	4·3	4·4	7·0	9·5	13·8	14·5	14·6	13·1	11·8	9·2	7·2
1955												
Air	2·4	1·1	6·4	8·8	9·1	12·9	17·5	17·1	13·2			
Lake, surface	5·4	4·1	3·1	6·7	10·1	14·5	19·3	20·4	16·5			
Lake, 6 m	5·4	4·1	3·1	5·8	9·1	13·6	14·7	18·5	16·3			

was found at Stanmore in 1955 and a simple annual cycle is always found in the populations of *P. fontinalis* in the Lake District.

THE LIFE CYCLE OF OTHER FRESHWATER PULMONATES

(*a*) Physa acuta *Draparnaud*

In Britain *Physa acuta*, a Mediterranean species, lives mainly in canals, reservoirs, hot-house tanks and other artificial habitats. Collections at the Brent Reservoir at Wembley, north-west London, during 1954 showed that in this habitat the snails had two breeding seasons in that year, the second, very much smaller, occurring in September and October. The majority of the snails, however, do not reproduce at this time and over-winter instead. In the Surrey Canal at Camberwell, south-east London, breeding snails were collected from late April until December. This species breeds much more readily in captivity than *P. fontinalis*, and, unlike the latter species, snails collected at any time of the year from the canal and kept in aquaria at room temperature developed rapidly, subsequently laying fertile eggs. The life cycle in this case seemed much more

plastic, and any sample always contained specimens over a wide size range. This is possibly due to the artificial conditions in the canal which receives various effluents and so may have its temperature raised at intervals. To observe this species under natural conditions a visit was paid in August 1954 to St Jean-de-Losne, Côte d'Or, France, where *P. acuta* proved to be abundant in the rivers, canals, ponds and lakes. A number of very large snails was found in the River Saône. In captivity these did not lay egg capsules and soon died. Great numbers of recently emerged snails were also present in a variety of habitats, being especially numerous in the Canal du Rhône-au-Rhin. The observations suggest that, in France, there is a simple, annual cycle with a single well-defined breeding period. It seems unlikely that the young snails hatching in August would be able to develop to sexual maturity before the winter, and the absence of any snails of intermediate size indicates that reproduction does not extend over a long period.

(*b*) Physa gyrina *Say*

DeWitt (1954a, b, 1955) has described the ecology and life cycle of *Physa gyrina* at Ann Arbor, Michigan, U.S.A. Oviposition took place in the spring, a water temperature of 10-12° C being necessary for its initiation. In a permanent pond, some of the snails which hatched reached sexual maturity by autumn, and a few collected in August and succeeding months laid eggs when kept in the laboratory. In most specimens, however, spawning was delayed by the low temperatures until the following spring. In a habitat 300 miles to the north of Ann Arbor oviposition began about 3-4 weeks later, a result which corresponds to the difference in the time of the breeding periods of populations of *P. fontinalis* at Stanmore and Windermere.

(*c*) Ancylus fluviatilis *Müller*

Hunter (1953) working on populations of *Ancylus fluviatilis* in Loch Lomond, has described a simple, one-year life cycle. The snails die after spawning, most of which occurs between 20 April and 16 June, although a few egg masses were laid until 26 July. This description corresponds closely with the life-cycle of *Physa fontinalis* in Windermere and especially significant are the slightly later breeding period and the single annual generation. Similarly in both *Ancylus fluviatilis* and *Acroloxus lacustris* (L.) shell sizes recorded from the south of Britain are markedly larger, and Hunter suggests that this might be due to either the difference in latitude or increase in the available calcium.

(*d*) Lymnaea truncatula (*Müller*)

Walton & Jones (1926) report that in *Lymnaea truncatula* the egg masses are laid in March and hatch in an average of 20 days, the young resulting from this spawning ovipositing during the first week of July. The ova from these snails hatch during the first week of August. *L. truncatula* was shown by these workers to be self-fertile and oviposition can begin at a shell length of 4·0-4·5 mm. The

data on growth-rates indicate that two, and perhaps three, generations occur between March and October.

It appears, therefore, that, amongst the members of the Hygrophila, there is a basic, one-year cycle, although variations occur. In *L. truncatula* and *Physa fontinalis* under favourable conditions a second generation is produced during the summer, and *P. gyrina* exhibits a similar tendency. The maximum length of life in these cases is 1 year, but Bondesen (1950), reviewing the literature on the length of life in the Lymnaeidae, cites evidence of *Lymnaea stagnalis* (L.) and *L. glabra* (Müll.) reaching an age of 2 years.

COPULATION IN *PHYSA FONTINALIS*

At the height of reproductive activity, when collections of *Physa fontinalis* were brought into the laboratory, snails often appeared to copulate with the first individual encountered, providing that they succeeded in climbing on its shell. Many snails could be seen at this time moving round the aquaria with their penes partly everted. Once on the shell of another snail, the animal functioning as a male moved to the left-hand side of its partner, its penis being everted and then withdrawn frequently. Eventually, the penis was inserted into the female orifice, but was frequently withdrawn and reinserted once or twice before copulation began. There is considerable variation in the length of time during which the penis is left in the vagina of the copulatory partner, but it is usually between $\frac{1}{2}$ and $1\frac{1}{2}$ h. Occasionally, it is withdrawn after 5 min, whilst in contrast times of up to $3\frac{1}{2}$ h were observed.

In samples of 100 snails brought into the laboratory in April and placed in 4-litre tanks, besides the numerous copulations involving two individuals, four or five copulatory chains were usually formed. In a chain each individual adheres to the left-hand side of the snail below it, functioning as a female to the individual above and as male to the one below. The maximum number of snails observed participating in a chain was five, but three or four was more usual. The formation of copulatory chains is probably favoured by the concentration of the snails in a small space, and it seems likely that chain copulation occurs less frequently under natural conditions; I have never observed it in the field. There are several descriptions of chain copulation among the Basommatophora, and it is mentioned as an unpublished observation by Bondesen (1950) for *P. heterostropha* (Say) and has been described in *Lymnaea stagnalis* by Baudelot (1863) and by Crabb (1927). Geldiay (1956), concludes that chain copulation is the rule in Windermere. There are several accounts of copulatory chains in the Lymnaeidae, especially *L. stagnalis* (Baudelot 1863, Crabb 1927) and these are listed by Bondesen. Precht (1936) describes reciprocal copulation in several species of the Planorbidae, but this was never observed by me in *Physa fontinalis* or *P. acuta*.

DeWitt (1954a) noted that the smaller individual of the copulating pair of *P. gyrina* functioned as the male, and Bondesen (1950) similarly remarks that generally in the Basommatophora the same arrangement occurs. Measurements with *P. fontinalis*, however, indicated only a slight tendency for the male individual

to be the smaller, and in chain copulation the different sized snails appeared to be assorted at random, with no tendency for the chain to be formed of successively smaller snails.

The factors which govern copulation proved difficult to analyse. Throughout the winter the male genital system is mature; yet copulation does not begin until the following spring when the female system is fully functional. DeWitt considers that in *P. gyrina* the water must rise to 8-10° C before the initiation of reproductive activity. *P. fontinalis* when collected during the winter and kept at about 18° C never copulated, indicating that temperature is not the only operative factor. A number of copulating pairs and one chain, however, were observed in the laboratory at 18° C in a sample of snails within 1 hour of collection at Stanmore on 1 February 1955, when the pond temperature was 7·4° C. This record of copulation was the earliest in the year ever noted during this investigation. None of these copulating snails (size 6·7-9·0 mm) proved on dissection to have a mature female genital system, and in many the oviduct was still undeveloped. These observations suggest that the absence of copulation throughout the winter, even under laboratory conditions at 18° C is not necessarily due to the immaturity of the female system of either or both the copulants.

As described above, a collection of snails brought into the laboratory during the breeding season produces copulating pairs and chains within an hour, and this intense activity usually continues for some 5-6 hours. If these snails are kept until they die, it is very rarely that further copulation is observed. This is not because *P. fontinalis* pairs only once during its life, nor is it due to advancing senility. Thus most of the snails which pair in the laboratory have a bursa copulatrix which is already filled with sperm, indicating previous copulation in the pond, whilst senile snails brought together in aquaria after collection in late May still proceed to pair.

Whilst temperature and the maturity of the genital system are fundamental factors, copulation can be produced most readily by a sudden environmental change. Although the snails rarely pair again in the laboratory, once the initial copulatory activity is concluded, it can be induced again after a few days by providing the correct external stimulus once more. For example in one collection, when the initial copulation had ceased, the snails were placed in separate containers where they were kept for a week. After this time, when most specimens had laid one or two capsules, the snails were reunited in a small tank containing fresh water. Within an hour, a second outburst of copulatory activity, including the formation of several chains, had begun. On the other hand, a week after copulation had ceased in another sample, the water in the aquarium was changed, the temperature raised, both suddenly and gradually and the aeration increased by bubbling air into the culture. These experiments were repeated using different samples of snails which had previously paired and varying the combination of stimuli, but in no case was a second outburst of copulatory activity induced. Similarly, variation of the light intensity had no effect. It might be tentatively concluded from these observations that the sudden congregation of snails is

sufficient to cause copulation, but it is doubtful whether this is often of any significance in natural conditions. By producing marked environmental changes artificially copulation can be induced much earlier in the season, as on 1 February. It is probable, however, that pairing in natural habitats is confined to the early part of the breeding periods, when the internal activation is highest, and may be repeated later in the season only by transference to the laboratory.

OVIPOSITION OF *PHYSA FONTINALIS*

In the pond at Stanmore, the egg capsules of *Physa fontinalis* were usually laid on the leaves of *Stratiotes aloides* and less commonly on plant debris and the leaves of *Elodea canadensis*, whilst at Lewes they were found on a variety of the water plants. In the laboratory *Physa fontinalis* laid regularly on the glass walls of the aquaria, but capsules were also found loose on the bottom and attached to pieces of *Elodea* and lettuce, on which the snails were feeding.

When brought into the laboratory, *Physa fontinalis* lays egg capsules during natural periods of reproductive activity only. This is in contrast to *P. acuta* which, under suitable laboratory conditions, can be induced to breed throughout the year, although in the field one, and occasionally two, generations are produced each year. Agersborg (1932) similarly found that a community of *P. gyrina* living in the waste water from a corn-manufacturing plant, where a temperature of 28-35° C was maintained, developed rapidly and bred throughout the year.

As described previously, the female system remains undifferentiated throughout the winter, and it is not until the warmer weather that growth recommences and oviposition begins. Unlike copulation, the initiation of oviposition is dependent upon complete sexual maturity. No form of artificial stimulation in the laboratory will induce oviposition in immature snails. Furthermore, maturity is not always correlated with shell size; very small (5 mm) specimens occasionally produce capsules which are generally small, but subsequent dissection and histological examination prove that the genital system is fully developed. In a normal environment, therefore, temperature is the basic, though indirect, factor governing oviposition, since it controls the rate of development, and this regulates the time of the spring reproductive period. In the summer it also appears that oviposition can begin as soon as the snails reach sexual maturity.

Apart from this, temperature can have a more direct influence, there being a minimum value below which oviposition does not take place. Snails collected in February, while still immature, were placed in a refrigerator and kept at 5° C until April or early May, when they died. During this time no egg capsules were laid, whereas control specimens kept at room temperature and observed in the field oviposited in April or early May, and continued to do so throughout May. Similarly, sexually mature snails collected in April and kept at 1°, 4° and 5° C all failed to produce egg capsules. In another series of experiments specimens of *P. fontinalis* were brought into the laboratory and placed in aquaria which were maintained at 18° C. The majority of the snails were shortly engaged in copulation, and by the following morning many had oviposited. The snails were then

transferred to a refrigerator and kept at 4° C when, apart from a few capsules produced on the same day, oviposition ceased. After 10 days the snails were returned to room temperature, and 3 days later capsules were again laid. When kept at 7-8° C, however, mature snails from the same sample continued to lay egg capsules, although much less frequently than the control specimens at a room temperature of 18-19° C. Field observations show that the water temperature in the pond at Stanmore in both 1954 and 1955 was 11° C when the first egg capsules were laid, and it appears, therefore, that temperatures between 7 and 11° C are critical in the initiation of oviposition.

Snails with a shell length of 7·0 to 8·3 mm were collected in October, when the water temperature was 12° C, and dissection of a selection of these confirmed that the female system was undeveloped. During the warmer weather in the summer snails of this size were almost invariably found to be mature and able to lay egg capsules. These immature specimens were kept in aquaria in which the water temperature was maintained at 22° C from October until January, by which time most of them had died. However, the behaviour of the snails agreed with those living in natural conditions in the pond at this time, and no egg masses were laid during this period. Similarly snails collected during January and kept at 22° C began ovipositing in April, about the same time as specimens in Stanmore Pond. These observations suggest that it is not only the low temperatures of winter which prevent egg-laying in *P. fontinalis* but that, in contrast to *P. acuta*, the annual pattern of development cannot be markedly altered experimentally to produce continuous reproduction.

A series of experiments has been performed by De Witt (1954a), working on *P. gyrina*, and by Cheatum (1951), working on *Lymnaea palustris*; in both these species, when specimens were collected in winter and kept at room temperature, oviposition began within a few hours. With such a short time interval both species, unlike *Physa fontinalis*, must be sexually mature at the beginning of the winter. However Precht (1936) found that *Planorbarius corneus* (L.) will not oviposit during October and November when kept at 23° C, although subsequently egg capsules were deposited at this temperature. Bondesen (1950) records that *Ancylus fluviatilis* will not oviposit below 7° C, and he was unable to obtain capsules from snails brought into the laboratory on 6 March, although a few small capsules were laid by snails collected 6 days later. It appears, therefore, that there is a marked difference in the developmental rate of the female tract in the different members of the Hygrophila.

Observations showed that specimens of *Physa fontinalis* kept in the laboratory oviposit at fairly regular intervals, generally every 2 to 4 days.

However, a subsequent change in the water of the aquaria was found to disturb the periodicity, causing a rise in the number of capsules produced during the following night. Linville (1900) also found that a change of water would cause oviposition in *Lymnaea elodes* Say. Raven (1948) describes experiments performed by Nieuwenhoven & Lever, in which oviposition was induced in *L. stagnalis* by the introduction of the water plant *Hydrocharis morsus-ranae* Linn. into the

aquarium. In the dark, *Hydrocharis* had no effect, although a short period of illumination produced a reaction. When the snails were placed in water saturated with oxygen the results were comparable to the introduction of *Hydrocharis*, and Nieuwenhoven & Lever conclude that the stimulation caused by this plant is due to the oxygen which it produces. The results are not entirely satisfactory, since no reaction was obtained if the snails were separated from the leaves by a piece of gauze, nor did the gradual increase of the oxygen content of the water or the addition of the water plant *Elodea* induce oviposition. They found, however, that a gradual rise in temperature from 18 to 28° C produced a strong reaction, and further that the time taken for the capsule to be deposited after the addition of *Hydrocharis* and the percentage of snails responding was proportional to the temperature.

It appears from the results obtained in this investigation that oviposition can be induced in mature *Physa fontinalis* by a variety of environmental changes which probably produce a rise in metabolic activity and so act as the releaser for the liberation of the ova from the ovotestis. It has been suggested that oviposition

Table 6. *Number of eggs per capsule laid by seventy-four* Physa fontinalis

For further explanation see text.

Oviposition	Number of capsules	Eggs per capsule		
		Max.	Min.	Mean
1st	74	27	0	11·5
2nd	72	17	2	8·4
3rd	63	16	1	7·3
4th	41	12	1	6·5
5th	23	11	3	6·0
6th	7	7	3	5·3

in the Basommatophora is dependent on copulation, which Baudelot (1863) suggested served to force the eggs out of the ovotestis. Copulation is not essential, however, since many species when bred in isolation from hatching can produce fertile eggs (Crabb 1927, DeWitt 1954b, Duncan 1958), but when specimens of *P. fontinalis* are brought into the laboratory from the field during the breeding season, oviposition is always preceded by intense copulatory activity. Oviposition by these snails then follows regularly, but after the initial outburst of activity copulation is rarely seen, so that it is possible that pairing may serve as a stimulus which is able to initiate oviposition.

In *P. fontinalis*, the number of eggs per capsule was found to vary considerably, and to investigate whether this fluctuation could be related to the size or age of the individual thirty-seven snails were kept in separate tanks in the laboratory and daily records were made of the egg capsules laid by each animal; the number of eggs in each capsule was noted. Following the initial outburst of oviposition, there is a progressive decline in activity, capsule deposition becomes more sporadic and fewer eggs are produced in each capsule. Table 6 gives an analysis of the capsules laid by seventy-four snails. The mean number of eggs per capsule falls

steadily from 11·5 at the first oviposition to 5·3 at the sixth. It can be seen, therefore, that when the animals are kept in the laboratory, the number of eggs in the capsule of *P. fontinalis* is not proportional to the size of the snail but depends on the time in the oviposition cycle of the animal. However, snails which lay egg masses during the second breeding season in August are always much smaller than the mature specimens found in the spring, and their capsules contain fewer eggs. W. F. DeWit (1955) claims that in *P. fontinalis* living under natural conditions there is a significant positive correlation between the number of eggs per capsule and the size of the animals. Thus, the animals of the spring generation are smaller and these lay fewer eggs. DeWit obtained these results by collecting egg capsules throughout the season and correlating the number of eggs per capsule with the shell length. However, the results recorded in this investigation, which show a progressive decline in the number of eggs per mass as the snail becomes older, were obtained by observing isolated snails which were kept in the laboratory and under artificial conditions. A similar decrease in egg production has been recorded in many species of the Basommatophora, the results being listed by R. M. DeWitt (1954b).

Table 7. *Periodicity in egg laying in* Physa fontinalis

The number of capsules laid at two-hour intervals by forty snails during one week.

Midnight	4	08·00	13	16·00	2
02·00	10	10·00	2	18·00	2
04·00	15	Noon	0	20·00	4
06·00	13	14·00	3	22·00	2
				Total	70

In a laboratory culture of breeding *P. fontinalis* there is a daily rhythm in oviposition, and the following experiments show that most egg capsules are laid in the hours between midnight and 8.0 a.m. About forty snails were kept for a week in a tank where they experienced the usual diurnal fluctuations in light intensity, and counts were made of the egg capsules deposited at two-hourly intervals. The results are given in Table 7 which show that 73% of the egg capsules were laid in the period between midnight and 8.0 a.m. Fifteen snails were kept in continual darkness in separate containers which stood in a lightproof tank, and another fifteen in a similar tank were subjected to continuous illumination by a fluorescent tube which was placed over a plate glass screen inside the tank. Two further tanks were maintained; the snails in one received the usual daily light fluctuation and in the other a fluorescent tube was switched on at night and off during the day when they were kept in darkness. The snails in this last experiment, therefore, received a reversal of the normal light fluctuation. No vegetation was placed in any of the containers and the temperature in all the experiments was found to fluctuate only very slightly. Observations were made at the same

time every night and morning and the egg capsules were marked and recorded. The results are given in Table 8; in both experiments the snails continued to lay chiefly at night. Thus, 86% of the capsules in experiment A and 85% in experiment B were laid at night. In the control experiment C, where 8 snails received the normal daily illumination, 78% of the capsules were laid at night. Similarly, in the experiment recorded in Table 7 with forty snails, 81% of the capsules were produced between 8.0 p.m. and 8.0 a.m. Finally, for the last 5 days of the experiments, twenty snails were kept in darkness by day and artificially illuminated at night (Table 8, D). Again, 78% of the capsules were laid during the solar night when the snails were illuminated. Cole (1925) also noted that *Planorbarius corneus* and *Planorbis trivolvis* Say continued to lay at night when subjected to continuous

Table 8. *Egg laying in* Physa fontinalis *under controlled conditions*

Figures show the number of egg capsules laid on successive days. For further explanation see text.

Day number	A – dark (15 snails)		B – light (15 snails)		C – control (8 snails)		D – reversed illumination	
	Night	Day	Night	Day	Night	Day	Night	Day
1	7	2	6	1	2	0	–	–
2	3	2	6	1	0	1	–	–
3	3	1	5	0	3	1		–
4	6	0	6	0	1	1		
5	4	0	1	2	3	0	–	–
6	4	1	4	1	1	0	–	–
7	3	0	1	2	1	1	–	–
8	2	0	1	0	0	0	–	–
9	5	0	8	1	1	0	–	–
10	1	0	1	0	0	1	9	2
11	1	0	1	0	4	0	3	2
12	3	1	2	0	1	0	6	1
13	5	1	1	0	1	0	4	2
14	3	0	1	0	0	0	3	0
Total	50	8	44	8	18	5	25	7
Percentage	86	14	85	15	78	22	78	22

light. In spite of all precautions to eliminate variable influences, this periodicity may be related to some uncontrolled factor in the environment, or may be regulated by an internal rhythm.

DISCUSSION

A study of the ecology and annual cycle of *Physa fontinalis* suggests a plasticity in the reproductive behaviour of this species. As an example the absence of a second breeding period in certain years and habitats may be instanced and also the variety of stimuli which may induce oviposition.

From the results described above, it was concluded that temperature is the most important basic factor governing the annual cycle of *P. fontinalis*. Thus, in this species, growth almost ceases at temperatures below about 7° C and R. M. DeWitt (1955) has recorded a similar cessation in *P. gyrina* at 10-12° C. In both

these species, snails living 250-300 miles farther north have a breeding season which is appreciably later than that of those living in localities in southern Britain or Michigan, U.S.A. In Britain this is probably due to the colder weather conditions, especially during the important months of April and May. During the summer months, the young snails develop rapidly, and under favourable conditions many reach sexual maturity in August when they lay fertile eggs. In the spring, when the water temperature rises above 7° C, the growth of *P. fontinalis* is renewed and the female system reaches maturity rapidly. The water temperature is therefore fundamentally responsible for the initiation of copulation and oviposition, so establishing the annual pattern of reproduction.

The male system only is fully functional during the winter, so that snails will not oviposit at this time, even when kept at temperatures of 15-20° C. However, the development of the female system in the spring causes the endogenous production and build-up of reproductive specific energy (following the terminology of Lorenz 1950). It is impossible to state what process is responsible for this increase of intensity of internal motivation and, as far as is known, the existence of hormones has not been demonstrated with certainty in the Pulmonata. However, Hanström (1939) records experiments, mainly performed by Hykes, which describe the effect of thyroxine and adrenaline on development and other physiological processes in certain gastropods. The results are not entirely satisfactory, but it seems probable that some form of hormonal control exists. It is hoped to begin a study of this and the nervous co-ordination underlying reproductive activities in the future. It is possible, however, that the increase in internal excitation is due to intrinsic factors within the nervous system and in support of this theory it may be pointed out that there is evidence, which is discussed below, of a basic rhythm which governs oviposition.

The existence of a build-up of action specific energy is demonstrated by the variation in response to certain stimuli as the breeding season approaches. Thus after a change of water and a rise of temperature to 15° C very few specimens of *P. fontinalis* were found to copulate and oviposit in early March, even though the genital systems proved to be mature on anatomical examination. However, samples collected at the beginning of the breeding season in April showed a tremendous outburst of copulatory activity, even when the snails were kept in the same water and were transported and maintained in the laboratory with no change in temperature. At this time, the snails were even observed moving around the aquaria with their penes everted and these observations indicate a lowering of the threshold of response.

Copulation and oviposition appear to be innate reactions and their initiation will therefore be governed by certain stimuli. Tinbergen (1951) concludes that in the case of innate reactions 'there must be a special neuro-sensory mechanism that releases the reaction and is responsible for its selective susceptibility to such a very special combination of sign stimuli'. This mechanism he calls the innate releasing mechanism. From the results of the present investigation it may be concluded that in *P. fontinalis* pairing in natural habitats is probably confined to

the early part of the breeding seasons, when the internal activation is at its peak and is repeated later in the season only by artificial stimulation. Copulation is most readily induced by a sudden congregation of the snails, and in a sample brought into the laboratory after the initial outburst of copulatory activity pairing could be started again only by separating the snails and subsequently reuniting them. However, it seems unlikely that this represents the innate releasing mechanism under normal conditions, where any environmental fluctuation will probably serve in the initiation of copulation. The results also suggest that there is no specific stimulus governing the beginning of oviposition. Once the action specific energy has built up to a maximum, it appears that any environmental variation, such as a rise in temperature or change of water, is sufficient to initiate oviposition. In experiments with *Lymnaea stagnalis* (Raven 1948) a gradual rise of temperature from 18 to 28° C or the introduction into the aquarium of *Hydrocharis morsus-ranae* produced a marked increase in egg-capsule production, a response which was not obtained by a gradual increase in the oxygen content of the water. In this connection, it is of interest to note that Orton, Southward & Dodd (1956) conclude that the spawning stimulus of the limpet, *Patella vulgata* L., is due to violent wave action caused by rough seas and onshore winds. In *Physa fontinalis* copulation may provide the stimulus necessary to initiate oviposition, but it is not essential, as snails bred in isolation are able to spawn without previous copulation (Duncan 1958). It seems probable, therefore, that the innate releasing mechanism for both copulation and oviposition is not rigid, but may be produced by a variety of stimuli.

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SUMMARY

1. In a population of *Physa fontinalis* studied in Stanmore Pond the majority of snails exhibit a simple annual cycle, the main period of reproductive activity occurring during April and May.

2. A proportion of the young snails which hatch in the spring reach sexual maturity by late July, when a second, smaller spawning ensues.

3. Immature snails exhibit a condensed protandric sequence. Throughout the winter the male system is fully functional whilst the female tract remains small and is difficult to distinguish in sections.

4. Temperature was found to be of fundamental importance among the factors affecting the life cycle.

5. It is suggested that certain environmental changes serve as the releasing mechanism for spawning.

6. In the laboratory the majority of egg capsules were laid during the period between midnight and 8.0 a.m. and experiments showed that this was not governed directly by light fluctuation.

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THE RATE OF DEVELOPMENT OF *BALANUS BALANOIDES* (L.) EMBRYOS *IN VITRO*

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(With 2 Figures in the Text)

The breeding season of a species is generally taken to mean the period during which a proportion, or all, of the population is in a reproductive state, either spawning or carrying embryos. During the breeding season any one individual may breed once or several times, according to the breeding habits of the species, while the proportion of breeding individuals present in the population may rise slowly or rapidly. If the time taken for the proportion of breeding individuals in the population to approach its maximum is short in comparison with the time of embryonic or larval development, the resulting embryos or larvae will develop more or less in step with each other; if not the embryonic or larval stages will overlap. If this overlap is considerable, and particularly if the individual produces several broods in a season, it may be very difficult to determine the time of embryonic development by serially sampling the larvae or embryos, and other methods of following the rate of embryonic development must be used.

The developmental stage of cirripede embryos can be judged in some species by observing the colour changes of the eggs through the base of the barnacle, but this is only possible if the adult will settle freely on glass and has a transparent base, as for example in *Elminius modestus* Darwin (Crisp & Davies 1955). However, this method does not allow detailed examination of the embryos, and is useful mainly in determining the number and frquency of broods per individual.

Since the embryos of cirripedes are carried freely in the mantle cavity, through which the sea water is regularly passed, there seems no reason why they should not develop in sea water *in vitro*. My first attempts using egg masses of *Balanus balanus* (L.) (= *B. porcatus* da Costa) were unsuccessful, probably because the adults and the eggs taken from them were not kept at a sufficiently low temperature. Later Clegg (unpublished observations) found that eggs of *Elminius modestus* developed from a fairly early stage (Stages 5-9, Crisp 1954) without difficulty and hatched. Subsequently, the eggs of *Balanus balanoides* (L.) were incubated *in vitro* with moderate success in spite of their long period of development, while all the egg masses of the summer breeding forms which have so far been tried have developed well in sea water. It is curious that Barnes also reports his failure to incubate cirripede eggs *in vitro* (Barnes 1957).

DEVELOPMENT *IN VIVO*

(*a*) *Rates of development in nature*

In Britain *Balanus balanoides* fertilizes during November. The onset of breeding is rapid, and, in a given locality, very regular. At Bangor, for example, over most

of the intertidal zone the process usually starts between 5 and 9 November and is nearly complete by 14 to 18 November. The main variation in the onset of breeding appears to be correlated with tidal level, as shown in Fig. 1. Thus if samples are drawn only from a given tide level, and preferably from one small area of shore, the variation in time of onset of fertilization between samples can be further reduced, and the accuracy of results obtained from serial samples may be improved accordingly. The time of development of a given stage can then be obtained from the results of serial sampling using the formula given by Crisp (1954). The methods employed for *B. balanoides* were those previously described, except that the barnacles were collected from the intertidal zone and were usually

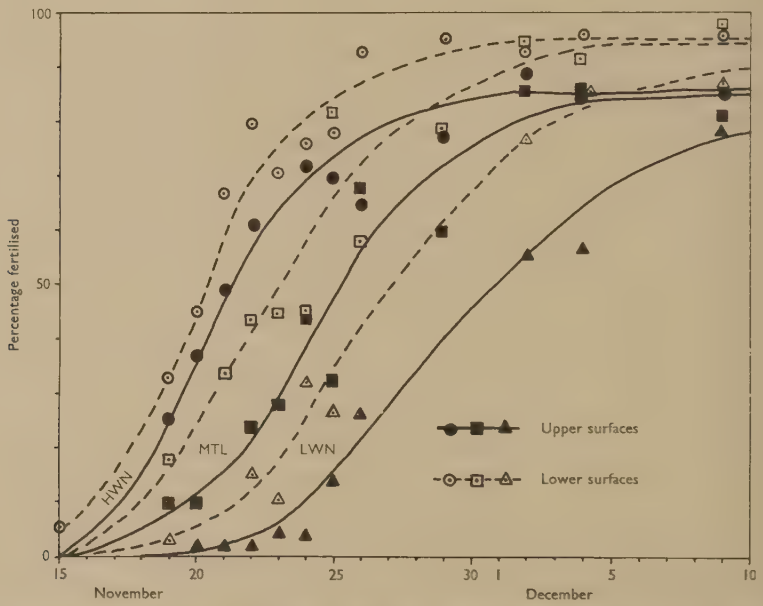

Fig. 1. Sequence of fertilization in *Balanus balanoides* collected from above and below boulders at three tidal levels on the shore. The higher barnacles, and those under stones are the first to become fertilized. Circles, HWN samples; squares, MTL; triangles, LWN samples.

examined fresh, within an hour of being collected. The stages of development were identical with those of *B. balanus* (Crisp 1954).

Table 1 gives the result of four sets of observations made during different seasons at Brixham (Devon) and at Bangor (Caernarvonshire). It is difficult to establish the accuracy of these results as they are liable to three independent sources of error: normal sampling variance, heterogeneity in the population sampled in regard to the distribution of age-groups of embryos, and errors of classification. The effect of heterogeneity can be overcome to some extent by increasing the sample size. This has been done in the case of columns 2 and 4; a series of observations at Brixham taken at three tidal levels involving some 150-200 individuals in

each sample were pooled in column 2 and a similar series at Bangor pooled in column 4. Nevertheless the results in column 5, which were obtained by taking much smaller samples of only fifty to sixty individuals every 1 or 2 days from a very limited and therefore more homogeneous population, are probably more accurate. Errors in classification arise because egg masses intermediate in development between two stages may be classified differently in samples examined at different times. However, the stages are quite distinct, so that embryos which are developing between stages n and $n+1$ would not be mistaken for any stage above $n+1$ or below n. Errors committed in this way will not therefore influence the cumulative development times of earlier or later stages.

The results for different seasons in the same locality show reasonably good agreement, especially up to stages 9-10, but there is a considerable difference between

Table 1. *Embryonic development in* Balanus balanoides (*L.*)

Each entry gives the estimate, from serial samples, of the time taken in days to develop beyond the stage given in column 1.

Stage of development	Brixham 1949-50 Mean of three tidal levels between HW and LW	Brixham 1950-1 HW level mean of two sets of observations	Bangor 1951-2 Mean of three tidal levels between HW and LW	Bangor 1954–5 Mean tide level in restricted area	Mean for Brixham	Mean for Bangor
1	0·65	0·80	1·4	0·93	0·72	1·16
2	1·85	1·2	1·5	1·46	1·52	1·48
3	2·4	2·7	4·4	2·72	2·55	3·56
4	3·15	3·2	5·1	3·5	3·18	4·30
5	4·9	4·5	6·3	6·3	4·7	6·3
6	6·8	7·8	8·8	10·7	7·3	9·8
7	14·4	12·8	19·9	21·0	13·6	20·5
8	24·7	19·0	27·2	31·7	21·8	24·5
9	33·1	29·7	52·7	51·4	31·4	52·0
10	41·4	33·5	72·0	58·7	37·5	65·3
11	50·9	41·5	97·3	76·8	46·2	87·0
12	61·2	53·0	108·4	101·1	57·1	104·8
13 (liberated)	96·9	82·8	148·9	139·8	89·8	144·3

the results at Brixham and those at Bangor, which can be seen from the mean values given in columns 6 and 7. The development times of the earlier stages, that is up to about stage 8, do not show appreciable divergence, but thereafter the rate of development of embryos in South Devon was nearly twice as rapid as their development in the Menai Straits. As a result, although fertilization takes place later in South Devon, the larvae are liberated into the plankton considerably earlier than they are in North Wales. Calculations of the rates of development at each of the three tidal levels were carried out on the sub-samples pooled in columns 2 and 4. The results, as expected, showed considerable fluctuations which tended to mask any trend. The values for the total time of development are given in Table 2, which includes also a series from Aberdeen which were not suitable for inclusion in Table 1. These figures indicate that embryos in the barnacles living

at high water generally take about a week longer to hatch than those at mean tide level.

(*b*) *Observations on* Balanus balanoides *grown on glass plates*

A small number of specimens of *B. balanoides* were allowed to settle on glass plates, and were maintained on a raft in Brixham Harbour as previously described for *Elminius modestus* (Crisp & Davies 1955). Observations were carried out at frequent intervals between November 1950 and April 1951, the behaviour of each individual being separately recorded. Half the individuals were fertilized by 30 November, and half were liberated by 28 March. The length of the early part

Table 2. *Time of development of embryos at three tidal levels*

Source of population	Total time of development (days) at			Difference from development time at MTL	
	HW	MTL	LW	HW	LW
Aberdeen, 1948-9	125	124	122	+1	−2
Brixham, 1949-50	103	96	92	+7	−4
	105	93	93	+12	0
Bangor, 1951-2	154	146	147	+8	+1
			Mean	+7	−1·25

of development, as judged by the change in colour of the egg masses from yellow to ochre and then to brown, agreed well with the results of Table 1. The mean time for the eggs to appear ochre was 33 days while the corresponding stage 9-10 is given in Table 1 as 29·7-33·5 days. The eggs observed on glass slides became brown after 54 days, while the corresponding stage 12 from the shore samples was 53 days. The total time of development up to release was, however, considerably longer in the group kept totally immersed on glass slides, 122 days as against 83. Moreover, the onset of liberation was both slower (Table 3) and less regular than

Table 3. *Phenological data for thirty-two* Balanus balanoides *observed individually growing submerged in Brixham Harbour*

Mean date of fertilization	30 November 1950	standard deviation	5·0 days
Mean date of release	28 March 1951	,, ,,	13·0 ,,
Mean time of embryonic development	122 days	,, ,,	14·5 ,,

the onset of fertilization, and no correspondence could be detected between individuals which were the first to be fertilized and those which were first released. In fact the variation in the times of development among different individuals was greater than either the variations between the dates of fertilization or the variation between dates of release (Table 3). These results accord with the view that the time of liberation is not dependent on completion of embryonic development, but is determined by an independent stimulus after a variable period of retention of fully developed embyros (Crisp 1956, Crisp & Spencer 1958).

DEVELOPMENT *IN VITRO*

(*a*) *Method*

The egg masses were removed from the parent barnacle and examined under a microscope. The stage of development of the embryos could usually be seen near the edge of the egg mass; if not the egg mass was discarded. Small, thin, egg masses in which many embryos could be observed clearly by transmitted light were preferred for these experiments. In egg masses which had developed beyond stage 6 the substance binding the eggs had become sufficiently friable for small pieces to be broken off with needles without damaging the embryos; pieces obtained in this way were also used. After removal, each egg mass, or piece thereof, was washed in gently running sea water for 15 min and transferred to a clean 3×1 in. specimen tube and loosely corked. Corks supplied nowadays with these tubes will freely admit air, and no further aeration was found necessary. The sea water in the tubes was changed daily, the egg masses being given two or three brief washes in clean sea water to remove completely any stale sea water occluded among the eggs. The tubes containing egg masses were kept in a thermoregulated space in a cold room at a series of different temperatures, and examined at intervals, daily or every 2 or 3 days, except near the end of development when the changes were slow.

The eggs did not develop uniformly; after a time those at the edge of the egg mass generally contained later stage embryos. The development of these outermost eggs was therefore recorded, rather than that of eggs lying in the centre of the egg mass which were in any case often obscured. Any eggs which showed abnormal development or which cytolysed were also ignored, and any egg mass which came to acquire a large proportion of such eggs was discarded.

Since only a proportion of the egg masses developed successfully from an early to a late stage of development, it was necessary to include in the results the normal part of the development of those egg masses which eventually had to be discarded.

(*b*) *Results of observations on development* in vitro

Since development was observed progressively in these experiments, a rough quantitative rating of stages was attempted; for example embryos which were half way between stage 4 and 5 were rated 4·5, when they had nearly reached stage 5 they were rated 4·8 and so on.

In this way it was possible by interpolation to estimate the time when each egg mass had reached the precise stage of development. These estimated times were then tabulated for each individual on the assumption that the time scale began with $t = 0$ at fertilization, the egg masses observed at their earliest stages being first entered on the table. The embryos observed from a later stage were then included, fitting the zero of the time scale so as to agree as nearly as possible with the previous entries in the table. The data from one series of experiments set out in this way are typified in Table 4. The mean values for times of development *in vivo* so obtained may be compared with the times of development of the natural population given in the bottom row of the table. At 6° C the early stages develop

Table 4. *Development times, in days at 6° C*

Expt. No.	Stage of development														
	1	2	3	4	5	6	7	8	9	10	11	12	13	A few hatching	Hatching complete
1		2·3*	3·2	5·0	..	..	..	..	..	..	..	..		..	..
2			3·3*	4·8	6·3	10·0	13·0	20	39	..	..	55	65	..	..
3				5·0*	7·0	10·0	..	..	..	..	..	..	..	..	..
4					9·0*	12·0	11·5	25	42	..	..			..	..
5						9·5*	14·0	25	39	47	53	58	67	79	
6							15·0*	22	38	50	58	64		..	
7								24*	34	52	49	63	72		
Mean	..	2·3	3·2	4·9	7·1	10·4	13·4	23	38	50	53·5	60	68	79	
Natural population (Bangor)	0·5	1·5	2·5	4·0	5·5	8·0	15·0	22·5	39	58	76	96	125		144

* Assumed value.

at a closely similar rate *in vitro* and *in vivo*, but the later stages appear to be telescoped into a shorter time *in vitro*. However, since only the peripheral eggs of the series observed *in vitro* were recorded, their more rapid development compared with those developing naturally is not necessarily true of the rest of the egg mass (see above). Egg masses raised *in vitro* appeared also to contain less brown pigment than egg masses taken directly from the mantle cavity at a corresponding stage of morphological development, but this appearance may also have been deceptive. The centre of the egg mass is not only less well developed but also less strongly pigmented than the outside when raised *in vitro*; naturally developed eggs appear to be more uniformly pigmented. Eggs developed *in vitro* hatched differently from those in the parent barnacle. Well developed egg masses did not hatch properly *in vitro*; usually one or two nauplii only were found hatched every few days

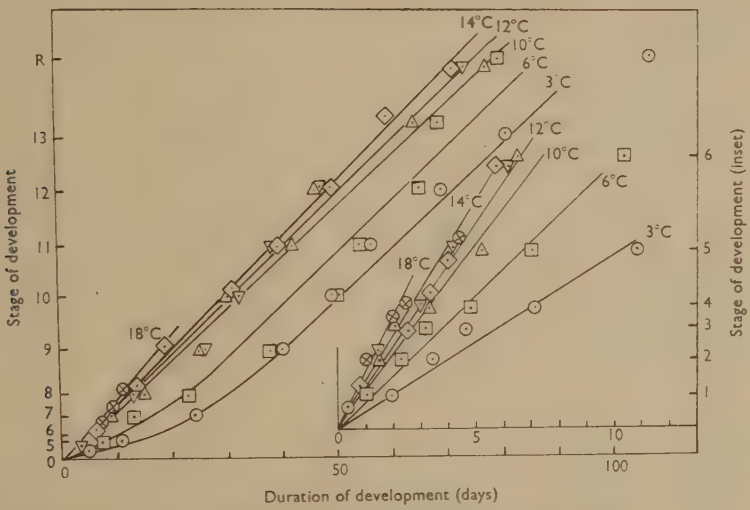

Fig. 2. Rates of development of the embryos of *Balanus balanoides* at a series of temperatures between 3 and 18° C.

whereas in the parent barnacle under natural conditions the whole egg mass hatched and the nauplii were liberated at once. This occasional hatching of one or two eggs at a time may have been due in part to differences between the development of eggs at the centre and of those at the periphery. However, it may also have been due in part to the need for a hatching factor, normally present in the mantle cavity of the adult at liberation, to stimulate the embryos to hatch (Crisp & Spencer 1958).

THE INFLUENCE OF TEMPERATURE ON RATE OF DEVELOPMENT

The rate of development of the peripheral eggs of *Balanus balanoides* at a series of temperatures is shown in Fig. 2. In order to convert the rates of development given in the ordinate as nearly as possible to a linear function of the time recorded

on the abscissa, the scale of stages of development has been adjusted so that each stage occupies a length proportional to its time of development under natural conditions as given by Table 1.

The influence of temperature is most clearly seen in the stages up to stage 8 where the limb buds first appear; thereafter the slopes of the curves do not differ very greatly. The delaying action of low temperature is not only confined to the early stages of development but is also most evident at temperatures below 10° C. The curves for development at 10, 12, 14 and 18° C are closely approximate, although at 18-20° C the eggs did not survive beyond stage 7. Evidently the rate of development approaches its maximum at 10° C and higher temperatures are ineffective in accelerating the process, if indeed they are not harmful.

The observations on rates of development at different temperatures permit a comparison to be made of development *in vitro* and *in vivo*, in which the temperature of the environment has been taken into account. Table 5 gives the time of development of embryos based on the data of Fig. 2, assuming that they were maintained at the same temperatures as given by the records for sea and air temperature at Brixham and Bangor for the relevant years. It will be seen that in

Table 5. *Development times* (*days*) in vivo *and* in vitro

		Brixham 1949-50	Brixham 1950-1	Brixham 1950-1*	Bangor 1951-2	Bangor 1954-5
Stage 9	Calc. (*in vitro*)	34·5	35	36	42	41
	Obs. (*in vivo*)	33	30	(33)	53	51
Stage 12	Calc. (*in vitro*)	51	50	52	66	65
	Obs. (*in vivo*)	61	53	(54)	108	101
Hatching	Calc. (*in vitro*)	69	73	75·5	79	78
	Obs. (*in vivo*)	97	83	122	149	140

* Continuously immersed.

the earlier stages, roughly up to stage 9 at Bangor and stage 12 at Brixham, the calculated times of development agree well with those obtained by sampling. The increased duration of the later stages does not therefore appear to be due entirely to the slowing down of development at lower temperature unless the effect of sudden cooling, or occasional sub-zero temperature, has a disproportionate effect on the rate of development. More probably some additional factor as well as temperature must be involved.

VIABILITY

Table 6 demonstrates how removal of egg masses at an early stage of development tends to prevent them from developing normally. When the egg masses were removed before reaching stage 3 a considerable proportion became completely cytolysed or abnormal before the end of development. Cytolysed eggs were often the site of an initial fungal attack which later spread through the rest of the egg mass and destroyed it. Eggs removed just after oviposition before the oviducal gland secretion had fully bound them together and hardened (stage 1) were especially liable to become abnormal. Degenerative changes were often accompanied by a breaking down of the whole egg mass into separate eggs, each still

encased in its shell. In some instances well-hardened egg masses containing later embryos were also found to have broken down in this way, presumably as a result of bacterial attack on the egg binding matrix (Barnes & Barnes 1955), but these later stage eggs developed quite normally notwithstanding. It therefore seems that freshly laid eggs are intrinsically labile and very liable to damage when removed from the mantle space. When removed at a later stage the eggs were much less susceptible to artificial conditions, and in fact all the egg masses which were removed after reaching stage 7 gave a high proportion of viable larvae if kept below 12° C.

Table 6. *Percentage of egg masses giving rise to viable larvae when removed from the mantle cavity and maintained at less than 12° C*

Stage of development when removed				
1	1-2	2-5	5-6	7 or later
20	62	63	87	100

Table 7 shows the relation between viability and temperature. 12° C appears to be the maximum temperature which the eggs can withstand for long periods without suffering damage.

Since *Balanus balanoides* often grows in estuarine environments, the salinity to which the developing eggs are exposed in the mantle space may sometimes fall. A few experiments were made to investigate the influence of lowering the salinity. Young egg masses between stages 2 and 5 were kept in sea water of salinity between 25 and 26‰ for periods of 1, 3 and 12 days, and then transferred to normal sea water of salinity between 34-35‰, their subsequent development being recorded. Of the egg masses kept only 3 days or less, the majority (80%) gave rise to viable

Table 7. *The influence of temperature on viability of egg masses of* Balanus balanoides *in vitro*

	Mean temperature of development (°C)							
	2·5	6	10	12	14	18	22	26
Percentage giving viable larvae	63	71	63	60	17	0	0	0
Maximum time of survival (days)	>91	>77	>72	>96	>77	37	18	10

nauplii, but there were in most cases a proportion of swollen and abnormal embryos. Of the four egg masses kept for 12 days all showed abnormal or abortive development, though one egg mass gave rise eventually to a few swimming larvae.

Development at higher temperatures results in smaller dimensions of eggs, larvae and adults in many invertebrates. Measurements were made on the hatched larvae to ascertain whether varying the temperature of development of embryos derived from similar egg masses had any influence on their ultimate size. Within the limits of the small numbers measured there was no significant difference

between those developed at 3° C, those at 14° C, and those hatched from the mantle cavity of barnacles which had over-wintered on the shore.

One interesting abnormality was noted in an individual egg developing at 12° C in an otherwise normally successful egg mass. In this egg part of the yolky vegetative pole material became accidentally detached at about stage 3-4. It rounded off, and lodged itself at the broad end of the egg. The remaining part of the egg continued to segment normally and gave rise to a tiny embryo at the narrow end. This embryo became fully developed, but did not hatch. The observation suggests that a considerable degree of regulation can take place in cirripede eggs early in morphogenesis. Abnormalities at later stages were not uncommon, but these gave rise to monstrous embryos.

RESPIRATION OF EGGS

As previously stated the outermost eggs were always more fully developed than the inner ones. Since the difference was more pronounced the larger the egg mass and the higher the temperature, it seemed likely that the inner eggs were being deprived of oxygen or perhaps were being slowed down by excess carbon dioxide. Thorpe & Crisp (1947) have given the equations for the diffusion of oxygen into respiring tissues in the case of a plane surface and a cylinder, and a parallel treatment can be applied for the case of a sphere of tissue. The fall in oxygen tension $\triangle p$ from the outside to the centre of a sheet of thickness $2t$, of a cylinder of diameter $2r_c$, or of a spere of radius $2r_s$ will be:

$$\triangle p \text{ (sheet)} = \frac{mt^2}{2P}, \qquad \triangle p \text{ (cylinder)} = \frac{mr_c^2}{4P}, \qquad \triangle p \text{ (sphere)} = \frac{mr_s^2}{6P},$$

where P = permeability of the tissue to oxygen, and m = respiratory rate of tissue per unit volume. The shape of the egg mass does not therefore alter the order of magnitude or the general form of the drop in tension. These relations may be used to estimate, in an egg mass of known dimensions, the maximum respiratory rate compatible with the centre of the egg mass being able to respire.

The diffusion constant D for oxygen in water may be estimated from the Einstein equation $D = RT\ 6\pi\eta\rho\ \mathcal{N}$ where R is the gas constant, T the temperature, $\mathcal{N}$ is Avagadro's number, η the viscosity of water and ρ the radius of the oxygen molecule. The value for D thus deduced is approximately 10^{-5} cm² sec or nearly 1 cm² day, and of the same order as the known diffusion constants for molecules of comparable size. From this and from the solubility of oxygen in water, the permeability of water to oxygen in ml sec cm² atm cm may be estimated. The value at 20° C is about 3×10^{-7} rising to about 5×10^{-7} at 0° C. We may take 6×10^{-7} as an upper limit for the permeability of the egg mass, assuming it is as permeable as water, and $2{\cdot}3 \times 10^{-7}$, based on Krogh's (1919) data for the oxygen permeability of tissues, as a more likely value. In air-saturated water the maximum permissible value of $\triangle p$ is 0·2 atm. Table 8 shows the maximum value for the respiration of the embryonic tissue which is compatible with the respiration

of the whole of the egg mass. The egg mass is treated as having the most favourable shape, namely a sphere, though it is more usually reniform. The respiratory rate of the egg mass of *Balanus balanoides*, according to Barnes (1957), rises from 2-3 µl of oxygen per hour per 100 mg of tissue to 10-14 µl per hour. This is equivalent in absolute units to a value of $0{\cdot}6\text{-}0{\cdot}9 \times 10^{-5}$ ml/sec/g rising to $2{\cdot}8\text{-}4{\cdot}0 \times 10^{-5}$ ml/sec/g later in development. The latter figure is of the same order as that for the adult barnacle, and for other crustacean tissues (Heilbrunn 1943, p. 259). Needham's (1933) data on the rate of oxygen uptake of the eggs of *Carcinus* has been

Table 8. *Maximum permissible rates of respiration*

Radius of egg mass r (mm)	Maximum respiration rate in ml O_2/sec/ml of tissue from $m = 6P.\ \triangle p/r^2$	
	Permeability $= 6 \times 10^{-7}$	Permeability $= 2{\cdot}3 \times 10^{-7}$
0·5	29×10^{-5}	11×10^{-5}
1·0	$7{\cdot}2 \times 10^{-5}$	$2{\cdot}8 \times 10^{-5}$
2·0	$1{\cdot}8 \times 10^{-5}$	$0{\cdot}69 \times 10^{-5}$
5·0	$0{\cdot}29 \times 10^{-5}$	$0{\cdot}11 \times 10^{-5}$
10·0	$0{\cdot}072 \times 10^{-5}$	$0{\cdot}028 \times 10^{-5}$

pooled and re-calculated (Table 9) to show its dependence on age and temperature. It can be seen that *Carcinus* eggs resemble those of barnacles in their increasing demand for oxygen as their development proceeds and more yolk is converted into embryonic tissue. Needham's figures for *Carcinus* show a considerable temperature dependence, but the high values obtained at 37° C are not within the normal physiological range of the animal. The results at 15° C, however, agree well with those obtained by Barnes for *Balanus* eggs, though an exact comparison is not

Table 9. *Mean respiratory rate of* Carcinus *eggs in ml O_2/g tissue/sec*

Data from Needham (1933)

Stage of development	*c.* 37° C	*c.* 15° C
Cleavage stages		
I and I, A	$4{\cdot}6 \times 10^{-5}$	$1{\cdot}4 \times 10^{-5}$
Intermediate stages		
II, III and IV	$11{\cdot}3 \times 10^{-5}$	$2{\cdot}8 \times 10^{-5}$
Late stages		
V, VI and VII	$23{\cdot}6 \times 10^{-5}$	$6{\cdot}1 \times 10^{-5}$

possible as Barnes does not quote the temperature at which his experiments were made. If we assume that the barnacle eggs require under natural conditions at least $0{\cdot}5 \times 10^{-5}$ ml of oxygen/ml of tissue/sec during early cleavage, and $2{\cdot}5 \times 10^{-5}$ ml/sec later in development, we may deduce from Table 8 that the thickness, or diameter of the egg mass must not exceed 2-3 mm. If it did, insufficient oxygen would diffuse to embryos at the centre of the mass, and their development would be retarded.

A reduced supply of oxygen in relation to the respiration needs of the egg mass would account for the difference in development between the inner and outer eggs,

but it is difficult to reconcile this explanation with the greater rate of development *in vitro* of the outermost eggs, compared with their average rate of development *in vivo*. It has been assumed, however, that oxygen can be carried through the egg mass only by diffusion. If the egg mass contains voids between the eggs through which water can percolate, the diffusion process may be considerably accelerated by convective transport. The adult is known to maintain a respiratory current by means of rhythmic movements (Crisp & Southward 1956), and these may help in circulating water slowly through the egg mass. At the same time the adult barnacle withdraws some oxygen for its own respiration through the gills and probably from the mantle lining. Hence it is possible that in the mantle cavity the eggs are maintained at a more uniform, though at a lower oxygen tension than when they are left in still sea water. The carbon-dioxide tension of eggs in the mantle cavity may also be higher, owing to the respiration of the adult, especially when the barnacle is out of water and respiring aerobically. High carbon-dioxide tension is known to slow down the respiration rate of some eggs (Burfield 1928, Root 1930).

RATE OF DEVELOPMENT, CLIMATE, DISTRIBUTION AND SIZE

The susceptibility of young embryos of *Balanus balanoides* to high temperature, and their failure to develop when maintained above 12° C (Table 5) is consistent with, and may be a factor controlling, the distribution of the species. The geographical range hardly extends south of the point where the winter maximum isotherm for sea temperature rises above 9° C (Hutchins 1947).

The influence of climate is also likely to be important towards the end of embryonic development. The time of development *in vitro* has been shown to occupy only 70-80 days, while *in vivo* it is considerably more prolonged. Although this is probably due in part to differences in the conditions, and needs further investigation, there seems little doubt that for some time after the embryos have reached full development in the mantle cavity they remain quiescent until hatching is eventually stimulated by a hatching factor (Crisp 1956, Crisp & Spencer 1958). Evidently during the period between the end of morphological development and hatching, the oxygen demand of the eggs is met. Perhaps the embryos enter a dormant state resembling diapause, perhaps also they tolerate a considerable degree of oxygen debt. In consequence they suffer no damage in the mantle cavity through lack of oxygen. However, Crisp & Spencer (1958) have shown that if the period of dormancy is unduly prolonged the brown pigment of the gut wall of the embryo changes to red or purple, probably through dissociation of a protein-astaxanthin complex, and the embryos soon die. Their death is thought then to be due to prolonged anoxia, and this is supported by the fact that such decomposition sets in first in the largest egg masses, and is least evident in small and thin ones (Table 10).

Calculations of the rate of diffusion of oxygen into egg masses (Tables 8 and 9) suggest that anoxia may easily occur if the rate of respiration of the eggs rises above a certain critical level. This is more likely to occur towards the end of

development, especially if the eggs are retained into late spring when higher temperatures prevail, unless some kind of dormancy supervenes to reduce oxygen demand. The limit to the size of an egg mass is therefore probably determined by the respiratory needs of the embryos at the end of development. If this is so, one would expect, in general, to find small egg masses in warm water species and large egg masses in cold water species. The very large size of many arctic barnacles with correspondingly large egg masses (e.g. *B. balanus*, *B. cariosus*, *B. hameri*, all of which may exceed 6 cm in basal diameter) and the generally small size of tropical barnacles, especially intertidal forms, seems generally to bear this out. Certain exceptionally large warm water species such as *B. perforatus* and *Tetraclita squamosa* may not possess such large egg masses as would appear at first sight, owing to the relatively great volume of their grossly thickened walls and the correspondingly smaller size of their mantle cavity.

Table 10. *Incidence (%) of decomposed egg masses in samples containing large and small individuals on 10 March 1957*

Samples were taken from an area facing south and protected from north and east winds after the exceptionally mild winter of 1956-7.

	HW springs	HW neaps	MTL	LW neaps, exposed to current	LW neaps in shelter
Large individuals, basal diameter >1·5 cm	0	0	23	45	91
Small individuals, basal diameter <1·5 cm	0	5	4	25	40
Increased incidence in large individuals	0	−5	+19	+20	+51

SUMMARY

1. Egg masses of *Balanus balanoides* and of other barnacles can be removed from the mantle space and allowed to develop in frequently changed sea water. The peripheral eggs may be observed continuously. The eggs lying at the outside of the egg mass kept in sea water develop up to a fairly late embryonic stage at the same rate as those retained naturally by the parent. Thereafter the eggs retained in the adult take longer to develop and hatch.

2. The stages of development, including cleavage, formation of blastoderm, and development of limb buds, are temperature dependent up to 12-14° C. The later stages, however, do not seem to develop much faster at 12° C than at 3° C. The sizes of the hatched larvae are unaffected by the temperature of development.

3. Eggs removed during cleavage are most liable to become abnormal and die, and eggs removed at later stages are progressively more hardy. Under the conditions of these experiments normal development of the egg masses is not possible at a temperature exceeding 12° C. A sea water of salinity 25-26‰ is not very harmful for short periods of the order of 24 h, but after 12 days in this medium development is seriously interfered with.

4. The eggs at the centre of an egg mass develop more slowly, and the theory is

advanced that this may be due to partial anoxia. Calculations indicate that the size of the egg mass is near the limit which permits oxygen to diffuse in sufficient quantity for the embryos growing in the centre of it.

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THE ANT-APHID-PLANT RELATIONSHIP IN WEST DUNBARTONSHIRE

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As part of an investigation of the eco-differentiation of ant species in west Dunbartonshire a survey has been made of the plants of the area which most commonly act as hosts to myrmecophilous aphids, and which are thus utilized by ant colonies to which they are a major source of carbohydrate and also a source of protein (Schmidt 1952). Apart from physical damage to the plant, caused by abstraction of sap and direct tissue destruction, the aphids and coccids act as vectors of various pathogenic organisms, virus, fungal and bacterial, and, where not closely attended by ants may provide the initial medium in the form of honeydew for the growth of sooty moulds (Carter 1933a, b, 1935, 1942, Serrano 1934). The term *myrmecophilous* is used here in its broad and somewhat misleading sense (Janet 1897), including as it does so many different types and grades of association, and also implying that the ants are actually sought out by the myrmecophile. Wasmann's term *trophobiosis*, described by Wheeler (1928), covering the particular type of association involving aphids and coccids, is much more descriptive and useful. The relations existing between aphids and ants seem to vary widely from intimate symbiosis to mere adventitious association, and while some of the aphid species listed in the present paper may not be accepted as obligatory trophobionts, they are at least tolerated and thus afforded passive protection. It is emphasized that this account deals solely with aphids found in the nest or adjacent galleries, and that more casual extra-nest associations, which are of little importance in this region in any case, are not considered.

METHOD

Aphid and plant samples from ants' nests were taken over a variety of habitats between Dumbarton and Glen Falloch. Equipment consisted of a trowel, sheath knife and fine forceps for excavation of the nest, with glass tubes and tins to contain aphid and plant specimens. All aphid samples, and most grasses, were identified in the laboratory, the aphids being preserved in the field in lactic alcohol. There was no emphasis placed on any particular ant species, thus the number of records for each ant and myrmecophile species is a broad indication of its relative abundance in the area. The islands in Loch Lomond were not included in the survey.

Leptothorax acervorum F. occurred frequently in the course of the investigation, but mainly as a plesbiont. In the few cases where isolated *Leptothorax* nests were investigated no aphids were found. As regards the other ant species, no aphids were evident in the nest itself in many cases at first, but during the examination,

which often involved the destruction of the fabric of the nest, they were usually discovered in one of the galleries, sometimes at a considerable distance from the nest centre. The number of nests which yielded no aphids formed about 12% of the total examined.

RESULTS

The results of the survey are set out in Tables 1 to 6. In the majority of cases (Table 2) the nests contained one aphid species on one food plant. In six cases the single species of aphid was spread over two food plants (Table 3). Twenty-two nests each contained two aphid species, and in two of these each aphid species was feeding on a different plant species (Tables 4 and 5). The maximum number of aphid species found in the same nest was three, which occurred four times (Table 6). In each of these four instances the three insect species were feeding on the same food plant.

Table 1. *The species recorded and their frequency*

ANTS		PLANTS	
Lasius flavus Fab.	62	*Agropyron repens* Beauv.	1
L. niger L.	3	*Agrostis alba* L.	86
Formica lemani Bondroit	119	*A. canina* L.	2
Myrmica lobicornis Nylander	1	*A. tenuis* Sibth.	68
M. rubra L.	65	*Aira caryophyllea* L.	2
M. scabrinodis Nylander	33	*A. flexuosa* L.	15
		Alopecurus pratensis L.	4
		Cynosurus cristatus L.	1
		Festuca ovina L.	15
APHIDS		*F. rubra* L.	50
Anoecia corni Fab.	48	*Holcus lanatus* L.	2
A. vagans (Koch)	1	*H. mollis* L.	13
Aphis craccivora (Koch)	2	*Molinia caerulea* Moench.	3
A. scorodoniae Del Gu.	2	*Poa pratensis* L.	12
A. tormentillae Pass.	1	*Juncus articulatus* L.	3
Baizongia pistaciae L.	1	*Luzula campestris* L.	4
Forda formicaria Heyden	154	*Potentilla erecta* (L.) Rausch.	1
Geoica pellucida (Buckton)	6	*Rumex acetosella* L.	3
G. setulosa (Pass.).	2	*Succisa pratensis* Moench.	1
Jacksonia papillata Theob.	1	*Teucrium scorodonia* L.	2
Rhopalosiphum insertum (Wlk.)	2	*Trifolium* spp.	3
Sipha glyceriae (Kalt.)	5		
Tetraneura ulmi (L.) Haliday	87		
Aphis confusa Wlk.	1		

It will be seen from Table 1 that the Gramineae suffer most as hosts of the trophobionts, especially *Agrostis alba* and *A. tenuis*, with *Festuca rubra* in third place. Lower in the scale, and all about the same level, come *Aira flexuosa*, *Festuca ovina*, *Holcus mollis* and *Poa pratensis*. The commonest triple association found was: *Formica lemani*, *Forda formicaria* and *Agrostis alba*, but it will be seen that the range in association is a wide one, and that a great degree of adaptability is evident in these relationships.

Forda formicaria was by far the most frequently occurring aphid, and the most polyphagous, with *Tetraneura ulmi* and *Anoecia corni* also prominent. Where,

Table 2. *Nests containing single aphid species on one plant species*

Figures in this and the following tables show the number of times each association was recorded.

ANTS	APHIDS	HOST PLANTS																				
		Agropyron repens	*Agrostis alba*	*A. canina*	*A. tenuis*	*Aira caryophyllea*	*A. flexuosa*	*Alopecurus pratensis*	*Cynosurus cristatus*	*Festuca ovina*	*F. rubra*	*Holcus lanatus*	*H. mollis*	*Molinia coerulea*	*Poa pratensis*	*Juncus articulatus*	*Luzula campestris*	*Potentilla erecta*	*Rumex acetosella*	*Succisa pratensis*	*Teucrium scorodonia*	*Trifolium* spp.
Lasius flavus	*Anoecia corni*	–	2	–	7		–	–	–	2	3	–	.	–	–	–	–	–	–	–	–	–
	A. vagans				–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
	Forda formicaria	–	10	–	2	2	–	–	–	–	3	.	–	–	1	–	–	–	–	–	–	–
	Aphis scorodoniae		–		.		–			–	–	–		–	–	–		.	–	–	1	–
	Geoica setulosa	.	2	–		–	–	–	–	–			–			–	–	–	–	–	–	–
	G. pellucida	–	3				.		–	–	–	–		–	–	–	–	–	–		.	–
	Baizongia pistaciae	–	1	.	.	–	.	–	–	–	–	.	–				–	–	–	–	–	–
	Tetraneura ulmi	–	2		3		2	–	–	1	3	–		–	1	–	.	–	.	–	–	–
Lasius niger	*Anoecia corni*	–	1	–		–	.	–		–	–	–	–	–			–	–	–	–	–	–
	Tetraneura ulmi	–	1		.			–	–	–	–	–	.	–	–	–	–	–	–	–	–	–
Formica lemani	*Anoecia corni*	–	1	.	4	–	–	1	–	–	4	–	1	–	–	–	–	–	–	–	–	–
	Forda formicaria	–	22	1	12		3	1	–	8	8	–	2	–	10	–	1	–	1	–	–	–
	Aphis craccivora	–	–				–	–	–	–			–	–	–	.	–	–	–	–	–	1
	A. tormentillae		–	–	.	–			–	–	–	–	–	.	–	–	–	1	–	–	–	–
	A. scorodoniae	–	.	.	.	.	–	–	–	.	–	–	–	–	–		–	–	–	–	1	–
	Tetraneura ulmi	1	5	–	2	.	7		–	2	7	–	1			–	–	–	–	–	–	–
Myrmica lobicornis	*Forda formicaria*	–	–	–	1	–	.	–	–	–	–	–			–	–	–	–			–	.
Myrmica rubra	*Anoecia corni*	–	–	–	8	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Forda formicaria	–	6		5		2	–	1	–	7	–	1	–	.	–	2	–	1	–	–	.
	Aphis craccivora		–	–	–			–	–	–	–	.	–	–	–	–	–	–	–	–	–	1
	Jacksonia papillata	–	–			–	–	–	–	.	–	–	–	–	–	1	–	–	–	–	–	–
	Rhopalosiphum insertum	–	1	–	–	–	–	.	.	–	–	–	–	–	–	–	–	–	.	–	–	–
	Sipha glyceriae	–	–	–	–	.	–	–	–	–	.	–	–	–	–	1	–	–	–	–	–	1
	Tetraneura ulmi	–	7	1	4	–	–	1	–	–	1	–	5		–	–	–	–	–	–	–	–
Myrmica scabrinodis	*Anoecia corni*	–	1	–	1	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–
	Forda formicaria	–	3	–	8	–		–	–	1	3	–	–	2	–	–	.	–	–	–	–	–
	Aphis confusa	–	–		–	–	–	–	.	–	–	–	–	–	–	–	–	–		1	–	–
	Sipha glyceriae	–	1	–	–	–	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Tetraneura ulmi	–	5	–	3	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–

Table 3. *Nests containing single aphid species on two plant species*

ANTS	HOST PLANTS: *Agrostis alba*	*A. pratensis*	*Festuca rubra*	*Holcus mollis*	*Luzula campestris*	*Rumex acetosella*	APHIDS
Formica lemani	1		1				*Forda formicaria*
F. lemani	1		1				*F. formicaria*
F. lemani	1					1	*F. formicaria*
Myrmica rubra		1		1			*Tetraneura ulmi*
M. rubra	1				1		*Forda formicaria*
Lasius flavus	1		1				*Geoica pellucida*

however, the vegetation type is completely unsuitable, even for these polyphagous and highly adaptable species, other species are usually available to take up the role of adventitious trophobiont. A striking example of this was noted by the author on the Isle of Mull, where large thriving colonies of *Lasius niger* (an ant rare in

Table 4. *Nests containing two aphid species on one plant species*

ANTS	APHIDS: *Forda formicaria*	*Tetraneura ulmi*	*Aneecia corni*	*Rhopalosiphum insertum*	*Siphα glyceriae*	*Geoica pellucida*	HOST PLANTS
Formica lemani	1	1					*Aira flexuosa*
	1		1				*Agrostis tenuis*
	1	1					*Festuca rubra*
		1	1				*F. rubra*
	1	1					*F. rubra*
	1	1					*F. ovina*
	1		1				*Holcus mollis*
Myrmica rubra	1			1			*Agrostis alba*
	1		1				*A. tenuis*
	1	1					*A. tenuis*
	1	1					*Festuca rubra*
	1	1					*Holcus mollis*
M. scabrinodis		1			1		*Agrostis alba*
Lasius flavus		1	1				*A. tenuis*
	1	1					*A. tenuis*
		1	1				*A. tenuis*
	1					1	*A. alba*
	1	1					*Festuca rubra*
	1		1				*F. rubra*
L. niger		1	1				*Agrostis alba*

Dunbartonshire) were found associated with *Aphis newtoni* Theobald for which the ants had constructed earthen shelters round the bases of the leaves of *Iris pseudacorus* L.

Aphids were most numerous and obvious in the nests in spring and autumn. In early summer *Formica lemani* and *Myrmica rubra* have been observed removing *Forda* individuals from the nest and releasing them in the open. Both *Forda* and *Tetraneura* have been seen wandering on the turf surface during the summer, free

Table 5. *Nests containing two aphid species on two plant species (each on a different plant species)*

ANTS	APHIDS	HOST PLANTS
	Tetraneura ulmi	*Agrostis alba*
Myrmica rubra	*Sipha glyceriae*	*Juncus articulatus*
M. scabrinodis	*Forda formicaria*	*Molinia coerulea*
	Anoecia corni	*Agrostis tenuis*

from any regimentation. Adult viviparae of these two species appear on the grass rhizomes near the surface layers of the nests in early spring, then the population builds up rapidly. While *Forda* and *Tetraneura* thus appear to overwinter as viviparous females deep in the ant galleries, *Anoecia* does so in the egg. Eggs of *Anoecia* are collected, by *Lasius flavus* at least, and in spring are placed in small piles in insolation sites. They hatch in mid-April. In North America, however, *Anoecia corni* is said to overwinter in the adult state (Cutright 1925).

Table 6. *Nests containing three aphid species on one plant species*

	APHIDS				
ANTS	*Forda formicaria*	*Tetraneura ulmi*	*Anoecia corni*	*Geoica pellucida*	HOST PLANTS
Formica lemani	1	1	1		*Festuca rubra*
Lasius flavus	1	1		1	*Agrostis alba*
L. flavus	1	1	1		*A. alba*
L. flavus	1	1	1		*A. tenuis*

The nectaries of *Potentilla erecta* are also very attractive to ants as a source of sugar. Workers of *Myrmica rubra*, *M. scabrinodis* and *Formica lemani* have been seen frequenting these flowers and occasionally gripping the base of the styles and pulling, as though attempting to carry the sugar source back to the nest. Seeds of *Potentilla erecta* and *Luxula campestris* are carried back into the nest, however, the latter being carried by the convenient basal appendage, but no evidence is yet available to show that these are used as food.

The only predators seen attacking aphids in the nests were syrphid larvae. Many of the aphid species listed also occur as pests of wheat and other cereals (Davidson 1925). The coccids *Orthezia cataphracta* Shaw and *Ripersia* spp., have also been found in association with ants in the area covered, but the importance of these in the food economy of ant colonies is probably realized, in this district, only in Callunetum, and is still being investigated.

DISCUSSION

The four common ants, the seven common plants and the three common aphids are considered specially. On ranking the 'choices' of the ants for grasses and for aphids, and the 'choices' of the aphids for grasses, then applying tests of concordance, it is found that there is significant concordance in all three cases. Further, on comparison of the ant and aphid ranking of plants (Table 7), it is seen that there is close agreement. Bearing in mind the polyphagous nature of the aphids dealt with, it is difficult to accept the hypothesis that four ant species and three aphid species may discriminate identically between seven plant species. The associations between ant and plant, and aphid and plant would therefore appear to be determined by the composition of the sward. As regards the ant-aphid association,

Table 7. *Ant and aphid ranking of grasses*

Grass	Ant ranking	Aphid ranking
Agrostis alba	1	1
A. tenuis	2	2
Aira flexuosa	5	5·5
Festuca rubra	3	3
F. ovina	4	4
Holcus mollis	6·5	5·5
Poa pratensis	6·5	7

on the other hand, the concordance shown is again consistent with a random hypothesis dependent merely on aphid population density, but since these aphids occur only in association with ants there must be some explanation of the different population strengths. These are most probably due to one or more extraneous ecological factors, such as minute differences in microclimate, as any active preference on the part of the host would lead to drastic reduction in number of the less popular myrmecophiles.

In general there appears to be little specificity in the relations between Homoptera and the ants attending them. Strickland (1947) has shown that the cacao mealybug *Pseudococcus njalensis* Laing is attended by fifty species of ants. Jones (1929), working in Colorado, found that *Formica fusca* var. *neoclara* Emery attended forty-two species of aphid representing five genera, and *F. fusca* var. *argentea* Wheeler thirty-one species representing fourteen genera (Nixon 1951).

Notwithstanding this apparent broad plasticity of ant-aphid association, Way (1953, 1954a, b) has demonstrated the high degree of interdependence which may

be evolved in one of these relationships. In the insects which he studied, *Oecophylla longinoda* (Latr.) and the coccid *Saissetia zanzibarensis* Williams, he found that the coccid and other honeydew-producing homoptera were the principal food source of the ant. Deprived of these, *Oecophylla longinoda* can exist only at relatively low population levels. Conversely, the size of the *Saissetia zanzibarensis* population is dependent on the level of the ant population, excess coccids, both nymph and adult, being attacked and killed. Although the host plants suffered obvious feeding damage under confined experimental conditions, this was not observed in the field, as *Oecophylla longinoda* farmed out the coccid nymphs, and maintained clusters on the host-plant twigs at a non-injurious level.

El-Ziady & Kennedy (1956) have found a similar relationship between *Lasius niger* and *Aphis fabae* Scopoli as regards the aphid population level, but there is no active farming in this case, the aphids being allowed to wander freely. While the latter authors did observe a certain amount of active protection of the aphids by *Lasius niger*, they incline to the view that any benefits thus derived are mainly secondary in importance to the possibility suggested by Herzig (1937) that in ant-attended aphid colonies the increased growth is a result of the greater intake of food due to stimulation of secretion. Kennedy & Mittler (1953), however, have shown that the rate of flow of phloem sap through the severed mouthparts is very similar to the rate of excretion of honeydew by the intact insect, suggesting that, in fact the aphid exercises little control on the flow of sap through its body, this being dependent mainly on the turgor pressure of the plant.

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SUMMARY

1. A survey was carried out of the aphids and their host-plants which are associated with ant colonies in west Dunbartonshire. Six ant species, fourteen aphid species and twenty-one plant species were recorded. Of these, four ant species, three aphid species and seven plant species occurred much more frequently than the others.

2. In this area there is no narrow specificity in the relationships between the common trophobiont myrmecophiles, the ants attending them and the host-plants, and so the ant-aphid-plant relationship plays no obvious part in the eco-differentiation of the four main ant species.

3. Grasses are the main plants which are exploited, the species utilized being determined mainly by availability corresponding to sward composition.

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POLYMORPHISM IN THE SURFACE WATER BUGS (HEMIPT.-HETEROPT: GERROIDEA)

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Many species of surface water bug exhibit a bimodal polymorphism of the alary apparatus, and occur commonly as small, isolated populations convenient for study. The present work describes an investigation into the determination and maintenance of this polymorphism. The polymorphism takes the form of differences in the completeness of the skeleton, muscles and nerves of the alary apparatus, and this is reflected in the length of the wings as compared with those of the fully winged or macropterous form (Ma). The differing degrees of wing reduction may be roughly defined as: brachypterous (Br)—wing length $\frac{1}{2}$-$\frac{2}{3}$ fully developed wings; micropterous (Mi)—wings $\frac{1}{4}$-$\frac{1}{3}$ of the length of fully developed wings; or apterous (Apt)—wings not visible externally. The short-winged forms are usually found on dissection to have no wing muscles and reduced pterophragmata.

The first important work on polymorphism in water bugs was carried out by Poisson (1924), and consisted of breeding experiments using *Gerris lacustris* Linn. He concluded that brachyptery was dependent on a single genetic factor dominant to that for macroptery with little or no environmental interference, despite certain well-marked disturbances of the genetic ratios. He made few observations on wild populations. Ekblom (1928, 1941) has dealt with several aspects of the biology of *Gerris asper* Fieb. Progeny ratios from a large number of breeding experiments were extremely variable but demonstrated in a general way the dominance of the short-wing factor. The apterous condition showed incomplete dominance to macropterous. Ekblom admits the possibility of environmental factors in determination; he describes the macropter as the summer form and the apter as the winter form.

Work on seasonal history with some reference to polymorphism has been done by Jordan (1943), Förster (1954) and Mitis (1937). From these results it appears that two complete generations per year for the subgenus *Limnotrechus* and one generation for the subgenus *Aquarius* seem probable. Short-winged forms are commoner in midsummer populations than at other times except in *Gerris asper*, where the reverse is true (Ekblom 1928).

It is convenient for both practial and theoretical reasons to divide the problem of polymorphism into two aspects: determination, the proportional effect of genetic and environmental factors in producing different forms, and maintenance, the effect of differential mortality factors ensuring the survival of more than one form. Whilst information on determining factors may be obtained from genetic, ecological and developmental work, maintaining factors must largely be discovered

by field work, although anatomical differences between the forms may suggest selective advantages. In this work, most results were obtained from field studies, and although some interesting progeny ratios were obtained from breeding experiments, these were fewer than intended owing to technical difficulties encountered in keeping the animals alive.

Five Gerroid families are represented in Europe, the Hydrometridae, Gerridae, Veliidae, Mesoveliidae and Hebridae, but while some observations were made on all these, most work was done on the Gerridae whose ten species exhibit a varied condition of the wing apparatus.

ECOLOGICAL OBSERVATIONS ON DETERMINING FACTORS

The work described in this section investigated the seasonal and geographical variation of the polymorphic ratio. Material was collected from England, western France and northern Spain. For purposes of conciseness collecting figures have been grouped according to the main trends observable.

(*a*) Gerris lacustris *Linn.*

It was clear from total field collections made from March to October 1953 that the Br forms were comparatively scarce during the first half of this period, but subsequently became much commoner: 1 March-1 July—31 Br : 427 Ma (1 : 14) (18 habitats); 1 July-30 October—66 Br : 139 Ma (1 : 2) (13 habitats). Unfortunately it was impossible to keep a monthly record of *G. lacustris* as the numbers from any individual habitat in the London area were small, *G. odontogaster* Zett. being the dominant species. Figures for the whole year from the London area, however, agree with those from total collections, though the variation in the polymorphic ratio is even more sharply diphasic: 1 March-1 July—4 Br : 191 Ma (1 : 48); 1 July-30 October—36 Br : 72 Ma (1 : 2). That there may be a falling off in the numbers of brachypters towards the autumn is suggested by these figures from the London area: July-August—55 Br : 102 Ma (1 : 1·9); September-October—26 Br : 72 Ma (1 : 2·8). This trend is shown more convincingly in samples from a small *G. lacustris* population living on the Radlett (Herts) gravel pit ponds: April—2 Br : 38 Ma; July—19 Br : 19 Ma; September-October—5 Br : 18 Ma. That the ratio varies in a similar way over a wide area at any particular time is shown by these two collections: western France and northern Spain, 17 March-20 April 1953—27 Br : 236 Ma (3 : 9); Penzance, Cornwall, August-September 1952—32 Br : 67 Ma (1 : 2). These ratios concur with those from total collections.

It appears from these figures that the polymorphic ratio may vary from 1 : 48 in the spring to 1 : 1 in the middle of the summer, and fall to 1 : 3 in the autumn. This variation indicates an alternation of summer brachypters with over-wintering macropters. Furthermore it suggests the presence of seasonally varying determinants of an environmental nature.

(*b*) Gerris asper *Fieb.*

This species occurred in only small numbers in collections made during 1952 and 1953, but the following records were made:

		Apt : Ma
North-west and central France	April	42 : 8
Hitchin, Herts.	June	21 : 0
Malham, Yorks.	September	10 : 0
	Total	73 : 8 (9 : 1)

These figures show that the apterous form predominated, the macropterous being only collected in the spring. If there is an alternation of forms as observed in other species, then it would seem probable that the apterous form is the dominant and over-wintering form, existing with a weakly developed macropterous population in the spring.

Mr E. S. Brown has kindly allowed me to use the following unpublished records for this species, collected in England, Wales and Scotland from 1941 to 1949; only the Scottish records cover the whole year: April –7 Apt : 19 Ma; May-July - 11 Apt : 8 Ma; August-October—15 Apt : 1 Ma. These results agree with those from France and England in that macropters are more abundant in the spring, but they appear to be altogether more numerous in these collections. Records for East Anglia in April and May, however, indicate that even at this time the macropters are scarce in a more southerly habitat: April-May—32 Apt : 1 Ma. In order to investigate the change in the polymorphic ratio in more detail than was possible in southern England, collections were made in 1956 from a small stable population in the vicinity of Windermere, Westmorland. The Congo Carr site consisted of small permanent pools on marshy ground near the mouth of the Blelham Beck. Monthly figures then were: April—12 Apt : 12 Ma; June –10 Apt : 16 Ma; July—10 Apt : 3 Ma; August—31 Apt : 3 Ma. These figures agree with those already given in suggesting the early development of the long-winged population, though the period of greatest numbers is early June rather than April or May. It seemed possible that the sheltered situation of Congo Carr might explain this difference. However, small collections that were made from exposed tarns near Windermere did not show this, macropters being altogether much rarer: April—16 Apt : 2 Ma; June 4 Apt : 1 Ma. It may be concluded from these records that the macropterous form is the summer form in this species, but that it appears to have its greatest development in April and June as compared with July in other species. The long-winged form seems to be uncommon in central and southern England, only one example in sixty-three apterous insects, but it must be pointed out that this species is peculiarly difficult to collect owing to its cryptic habits.

(*c*) Gerris odontogaster *Zett.*

This species was not thought suitable for study at the beginning of this work as it was generally recorded as rarely polymorphic in Great Britain. It was found to be the dominant pond species in the London area and Sussex, and at Radlett

(Herts) gravel pit ponds, where large numbers could be captured, a midsummer micropterous population was strikingly developed in 1953-4 (Table 1). Nymphs were not seen on the water until the middle of June when all stages were found; the first adults must have appeared between the last week in June and the first week in July. The micropterous population dominates in July, but falls off in August and September with the appearance of the new macropterous over-wintering forms.

A similar July micropterous population was observed in Southern Sussex: at Wick Farm—54 Mi : 7 Ma; and at Ditchling—24 Mi : 3 Ma. The Radlett and Sussex ponds all possessed a large *G. odontogaster* population, though the Radlett ponds were rapidly changing to marshland in 1954 following local drainage. The collecting records for this species clearly suggest extrinsic seasonal determinants of wing length.

(*d*) Gerris argentatus *Schum.*

This species resembles *G. odontogaster* in colour, form and polymorphism. It was found very abundantly in western France but only collected in the spring. In Great Britain it was found to be local and not very abundant.

Table 1. Gerris odontogaster *from Radlett, Hertfordshire*

	April		May		June		July		September		October	
	Mi	Ma	Mi	Ma	Mi	Ma	Mi	Ma	Mi	Ma	Mi	Ma
1952	–		–		–		–		–		0	21
1953	0	110	–		–		73	9	22	174	0	46
1954	–		0	52	0	71	76	6	–		–	
Totals	0	110	0	52	0	71	149	15	22	174	0	67

In the Sussex-London area in 1953 the ratios were: May—0 Mi : 23 Ma; July—9 Mi : 9 Ma; October—1 Mi : 28 Ma.

Figures from western France (0 Mi : 1 Br : 151 Ma) merely confirm the spring absence of short-winged forms (the brachypterous insect is uncommon).

BREEDING EXPERIMENTS ON DETERMINATION

Since the field observations indicated seasonal changes in the polymorphic ratio, it was necessary to attempt to find out whether the offspring of selected parents departed from the polymorphic ratio expected from Poisson's simple monohybrid theory, in the presence of environmental changes of a similar nature to those occurring in the field. Breeding was found to be only moderately successful owing to the accumulation on the water surface of airborne detritus (the experiments were carried out in the London area), cannibalism, excessive humidity and seasonal rarity of some forms. Ordinary glass-sided aquarium tanks were used with glass covers supported by cork struts 1 in. above the rim to ensure adequate ventilation. These were kept in a sheltered aquarium room in which the temperature varied little about 18 ° C, or out of doors in sheltered situations. The

tanks were about one-quarter filled with water and aerated with a bubbler to destroy surface scum by agitation and maintain submerged eggs.

The insects were fed at the rate of one blowfly (adult *Calliphora* or *Lucilia* spp.) per five gerrids per day — medium diet, or one blowfly per gerrid per day—maximum diet. The abbreviations Ma, Br., etc., describe phenotypes except where expressly stated otherwise.

(*a*) Gerris lacustris

The Br × Br cross—brachypterous insects were found to be scarce in the London area in the spring, and the first individuals captured did not survive well and laid few eggs, so that it was necessary to keep several pairs together. These were kept in an outdoor aquarium. The adults were fed maximum diet, the nymphs a medium diet; five pairs gave ninety-six adults, 37 Br : 59 Ma.

These may be arranged according to date of emergence:

1-15 July—4 Br : 25 Ma; 15 July-15 August—3 Br : 13 Ma; 15 Aug.-7 Sept.—12 Br : 12 Ma; 7-21 Sept.—14 Br : 6 Ma; 21 Sept.-13 Oct.—4 Br : 3 Ma. Using the χ^2 test for deviation of the total ratio from Poisson's monohybrid ratio, with loss of all Br homozygotes (*i.e.* 2 Br : 1 Ma), then $P < 0{\cdot}01$. However, if only the three later sets of figures are used, $P > 0{\cdot}25$ for the same ratio, or there is a reasonable fit. Thus the polymorphic ratio altered significantly between July and October, showing a predominance of macropters at the beginning, but inclining to a 2 : 1 ratio at the end.

The Ma × Ma cross—an attempt was made to rear offspring from this cross under different conditions of temperature and light, and three experiments were made.

First, the offspring of three pairs captured in the field at the end of June were kept in an indoor aquarium sheltered from direct sunlight at a temperature which fluctuated around 18° C; the insects were fed a medium diet and emerged between 15 August and 15 September; the numbers were 24 Ma : 1 Br. Second, the offspring of four pairs captured in the field at the same time as those used in the first experiment were kept in an outdoor aquarium subject to conditions of light and temperature prevailing during July and August. Temperatures recorded were much more variable, ranging from 12° C to above 28° C in strong sunlight. The offspring were 34 Ma : 10 Br.

The results of these two experiments suggest that the second group were subject to brachyptery forming conditions. It could be suggested that some of these parents were genotypically Br, but this is to some extent allowed for by using more than one pair of insects as parents in each case. Following these results an attempt was made to influence the offspring of macropterous insects directly.

In the third experiment thirty first instar nymphs, the progeny of two macropterous pairs taken from the field in June, were reared on top of a slide-drying oven. They were illuminated continuously from above by a bench lamp giving a temperature of 31° C just above the water surface. The insects were fed a maximum diet; ten insects emerged after 21 days (nymphal life 33 days at 18° C), and they

were all Ma. The high mortality was apparently due to ecdysial accidents following premature hardening of the nymphal cuticle. The negative result of this experiment agrees with Poisson's work (1924), but it does not necessarily invalidate the light and temperature theory of determination advanced here. Determination may occur during embryonic development or be altogether too critical to be effected by the means employed in this experiment.

(*b*) Gerris asper

It was not originally intended to study this species as its distribution is northern in Great Britain (few records south of latitude 53° N). However, a small apterous colony was found in north Hertfordshire in 1953.

The Apt × Apt cross—eggs from four pairs were randomly divided into two batches and reared under different conditions. Group A were kept in well-illuminated outdoor aquaria and exposed to June-July temperatures fluctuating about 23° C. Group B were kept in shaded indoor aquaria where day-time temperatures averaged 18° C. Both groups were fed a medium diet. By the χ^2 test

Table 2. *Progeny of four pairs of* Gerris asper

	Group A		Group B	
	Ma	Apt	Ma	Apt
July	2	21	3	4
July-August	2	7	10	9
Total	4	28	13	13
Ratios	1 : 7		1 : 1	
	Total 17 : 41 (1 : 2$\frac{1}{2}$)			

groups A and B show significant divergences from Ekblom's ratio for this cross (1 Ma : 2·7 Apt), while the combined ratio A + B (1 : 2·41) concurs ($P > 0{\cdot}10$). Groups A and B differ significantly *inter se* ($P < 0{\cdot}01$). A bilateral divergence from Ekblom's ratio of 1 Ma : 2·7 Apt is visible, so that a certain amount of confidence may be reposed in the result. These results strongly suggest that temperature and illumination or both are determinant factors, wing-length being inversely proportional to temperature or illumination.

(*c*) Gerris odontogaster

From the first collections it was clear that macropterous *G. odontogaster* were the dominant gerrids of the London area, but since no short-wings were captured and other collectors recorded them very infrequently, no special attempt was made to breed this species. In July 1953, however, large numbers of micropters appeared in several populations under observation. The only rearing performed was from these summer micropters. Fifteen pairs taken from the field at Radlett were kept in an aquarium and fed a medium diet. The offspring were 133 Ma : 0 Mi. This result parallels field collections and shows an extreme example of phenotypic

reversal; indeed the change in the polymorphic ratio appears to be much more rapid and complete than it is in the other species.

DETERMINATION DURING DEVELOPMENT

Under this head is included information on the comparative growth and development of presumptive short-wing and long-wing nymphs. A considerable amount of work (to be published elsewhere) was done on nymphal development but only certain findings have a direct bearing on polymorphism, *i.e.* developmental differences that indicate or reflect the nature of determining factors. Under the same environmental conditions the nymphal life is shorter in short-winged than in long-winged forms. Thus in *G. asper* (58 individuals) the average nymphal period was 24 days for the micropterous and 29 days for the macropterous form at 18° C. This agrees with Poisson's figures for *G. lacustris* though in this species the nymphal life was longer at a lower temperature (12-14° C). Growth differences between the two forms appear at least as early as the beginning of the third instar. Comparison between the wing muscles and buds and nerves indicate a lesser degree of development in the short-winged than in the long-winged forms as early as the third instar, these differences becoming extreme in later instars. Alary structures continue to develop in both forms at a steady rate up to a few days before metamorphosis. In this pre-metamorphic period wing muscles degenerate in the short-winged forms, whilst in the long-winged forms rapid growth takes place. These observations indicate separate developmental paths in later nymphal life and probably earlier. Whilst some possibility of later determination may be admitted, straightforward curtailment of macropterous development giving short-winged adults appears most unlikely.

MAINTAINING FACTORS

Evidence from the breeding experiments of Poisson (1924) and Ekblom (1941) and those described here points to the rarity of polymorphic ratios attaining or exceeding 3 : 1 from the Br × Br cross, and therefore strongly suggests that some form of homozygous lethality acts as a check to the spread of the short-wing factor. Flightlessness must also act as a barrier to the absolute numerical dominance of the short-wing forms, except perhaps in the large apterous species *G. najas* Deg., which appears to have spread over a wide area by skating. The selective advantages of the short-wing form are less clear and may only be arrived at by a careful study of the overall biology of both poly- and mono-morphic species. Since the evidence for possible selective advantages is somewhat fragmentary, these are presented under subject headings.

(*a*) *Egg production*

Poisson (1924) stated that the Br form in *G. lacustris* laid more eggs than the Ma form, and that this was associated with an enlarged ovary occupying the site of the wing muscles. Egg numbers from breeding experiments do not confirm Poisson's first statement in any species, neither do Ekblom's figures for *G. asper*.

Furthermore careful dissection shows that the space available for ovary development is not necessarily smaller in the macropterous form, as the wing muscles are resorbed during the egg-laying period. In both *G. lacustris* and *G. asper* the body volume is larger and the leg muscles are smaller in this form than in the Br form, so that a larger ovary could be developed. In *G. odontogaster*, however, the Mi females appear to be rather larger than the Ma.

(b) Skating ability

Dissection demonstrates that the size and arrangement of the leg muscles in the short-winged forms of polymorphic species indicate a more powerful skating apparatus than in the fully winged forms. Field observations did not indicate that the short-winged insects could skate for longer or more swiftly than the macropters. It might be expected from this that collections of a polymorphic species such as *G. lacustris* would show the largest proportion of brachypters to come from flowing water, but this was not borne out by collections: running water—29 Br : 150 Ma (1 : 5); still water—80 Br : 434 Ma (1 : 5).

However, the usually apterous species *G. najas* is typically a stream form and

Table 3. Gerris thoracicus *from Britain and France, 1952-4*

	Numbers (*n*)	Sites (*s*)	*n*/*s*
Pools (200 sq. ft)	43	8	5·4
Ponds (20 000 sq. ft)	37	6	6·1
Ditches and rivulets (4 ft broad)	25	4	6·1
Rivers and streams	5	2	2·5
Lakes	4	2	2·0

can be observed to swim against the current for at least an hour without pausing. The leg muscles in this species are large and reduction of alary structures far advanced.

There is evidence that some of the long-winged monomorphic species tend to favour small bodies of still water, rather than lakes or streams, on which skating ability may be presumed to be of least, and flying ability of most, selective advantage. Thus *G. gibbifer* Schum. was found to be locally abundant in England and France, where 367 specimens captured in 1953 in the course of routine collection were distributed thus: pools (200 sq. ft)—179; ditches and rivulets (4 ft broad)—172; streams and rivers—16; ponds and lakes—0. This division into waters of different sizes indicates a preference for small waters. The pools and ditches were almost all (13/15) shallow and clear, with little marginal vegetation, a clean resilient surface film and a slight current flow. Two sites were impermanent pools formed by spring rains (twenty-two specimens).

Gerris thoracicus Schum. was never found very abundantly in the field, but details of 114 specimens collected from twenty-two situations between 1952 and 1954 in France and Britain are given in Table 3. A preference for small waters is shown here as with *G. gibbifer*. The small waters favoured by *G. thoracicus* are,

however, often turbid and sheltered with surface weed and scum, and no current. This slim-bodied species is a noticeably weak skater.

Mr E. S. Brown has pointed out that *Velia saulii* in which the polymorphic ratio is near 1 : 1 favours still waters, while *V. caprai*, which is usually apterous, is characteristic of streams. This was borne out in the present work: *V. saulii*—7 Apt : 5 Ma from a stagnant ditch; *V. caprai* 320—Apt : 0 Ma, almost all of these from small fast streams.

(*c*) *Over-wintering and cold resistance*

According to Ekblom the apterous form of *Gerris asper* over-winters and is relatively cold hardy. In *G. lacustris* and *G. odontogaster* cold susceptibility may limit the adult life of the short-winged forms. An attempt was made to test the relative cold hardiness of the two forms in these species (Table 4). The result of this experiment indicates that in *G. odontogaster* at least, the short-winged forms are less resistant to low temperatures than the macropters. However, it must be pointed out that the micropters were between 8 and 15 weeks older than the macropters. The dead macropters were all young unhardened specimens.

Table 4. *The resistance of* Gerris lacustris *and* G. odontogaster *to refrigeration for 10 days at 3-5° C*

	G. lacustris		*G. odontogaster*	
	Ma	Br	Ma	Mi
Original numbers	13	3	140	20
Died	2	0	15	19
Died (%)	(16)	–	(11)	(95)

(*d*) *Development time*

As pointed out under the heading on early development, the short-winged forms have a shorter nymphal life than the long-winged forms at a given temperature. This is a clear-cut advantage in numerical dominance.

DISCUSSION

Alary polymorphism is a common phenomenon in insects, possibly because in many insects the wings are used at infrequent intervals, so that provided that a gene population contains wing factors that are manifested at a certain rate or under certain conditions a large proportion of the insects may be flightless and the population as a whole suffer no great selective disadvantage.

Purely genetic determination may be the simplest polymorphic situation and the Coleoptera and Lepidoptera furnish examples of this. Jackson (1933) has demonstrated a dominant brachypter in the cursorial weevil *Sitona* similar to that of *Gerris lacustris*. Determination by largely environmental factors also occurs in many insect groups. In the Homoptera the lability of determination appears very great (Pesson 1951) and there is little conservation within a line. Larsen

(1931) states that in the heteropteran *Aphelocheirus* the adult wing-length was determined by the oxygen tension of the nymphal habitat. Perhaps some of the most important work from the point of view of alary polymorphism is that relating to wing mutants of *Drosophila*. Eker (1939) showed that temperature differences altered the expression of 'short-wing' in *D. melanogaster*. Modifications were maximal at 27° C, whilst the gene behaved as a lethal above 30° C.

The polymorphic water bugs fall naturally into two groups, the highly polymorphic species, *Gerris lacustris*, *G. asper*, *G. odontogaster* and *G. argentatus*, and the remaining Gerroid species which are only slightly polymorphic. The latter group, though useful for purposes of interspecific comparison, are difficult to investigate in any detail on account of the rarity of the secondary form. It is frequently so uncommon that it could be accounted for by occasional mutation, with perhaps a short life within the population as a rare recessive. Alternatively these individuals may result from slight lability towards the environment of a genetically homogeneous population. The highly polymorphic species in which the form ratio may approach unity were found much more susceptible of study. From breeding experiments on *G. lacustris* and *G. asper* it appears that whilst the monohybrid theory of Poisson (1924) may form a genetic basis for the polymorphism it is subject to considerable modification. Outdoor reared offspring of Br. *G. lacustris* show an increase in brachypters during the summer, and this is reflected in field observations. Field observations on *G. odontogaster* and *G. argentatus* showed a similar summer short-wing population, rather earlier and more isolated than that of *G. lacustris*.

There appear to be seasonally varying determinants, probably capable of phenotypic conversion from short-wing to long-wing in both directions. Seasonally varying factors are temperature, light, day-length, food and crowding. An attempt to determine Ma *G. lacustris* nymphs with high temperature and light intensity was unsuccessful, but offspring of the Apt *G. asper* cross did show a higher proportion of short-wings at high temperature and illumination than at low. As *G. lacustris* nymphs were subjected to continuous artificial illumination while the *G. asper* nymphs were reared in modified daylight, day-length may play a part in determination. Food and crowding may be associated factors. In *G. lacustris* and *G. odontogaster* high polymorphic ratio seemed to be correlated with large population. Kind and amount of food taken were not investigated and would be difficult to study precisely, though there is probably more surface food from both land and subaquatic sources in the hot months when the short-wing population is developed than at the beginning of the summer.

The trend from Ma to Br may be explained as environmental determination of Ma genotypes, and as orthodox genetic determination of progeny of insects phenotypically Ma but genotypically Br. The transformation from Br to Ma can also be postulated, though the evidence for it is slight, as apart from the inclusion of insects of the second category above, the offspring of the Br × Br cross in *G. lacustris* and of the Apt × Apt cross in *G. asper* do not fall much below a 2 : 1 ratio.

As far as the short-wing homozygote is concerned, no Br cross has given any-

where near a totally short-wing batch of offspring, and although the occurrence of 3 : 1 ratios suggests that they might reach the adult state, complete mortality of homozygotes would be masked by a 20% environmental conversion of Ma to Br. One may assume therefore a considerable degree of inviability in the dominant homozygote. This homozygous disadvantage suggests itself as a balancing factor, offsetting advantages possessed by the short-wing form, and so maintaining this balanced polymorphism (Ford 1945). It may be pointed out here that the genetic factor of wing-length might exist as a one or many gene difference, that is, as a single pleiotrophic gene, or as two or more genes closely linked. In *Drosophila* and other insects wing differences are often found independently of wing muscle differences, and Poisson (1924) claimed to have found forms with only one part of the wing apparatus reduced in *Gerris lacustris*. None was found in the course of this investigation, although macropterous females frequently had shrunken wing muscles during the period of greatest ovarian development. The importance of temperature resistance and high egg yield as short-wing advantages put forward by other authors was not supported by the freezing experiments, egg counts and examination of female anatomy described. Advantages suggested by the present work are: (i) relatively large leg muscles and concomittantly greater skating ability, skating migration, life on flowing permanent continuous waters, and possibly longer hunting periods; (ii) rapid nymphal development; (iii) possibly in *G. asper*, life on weed-choked waters.

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SUMMARY

1. Field collections showed that the polymorphic ratio varied seasonally. In *Gerris lacustris*, *G. odontogaster* and *G. argentatus* there is a summer short-wing trend and a winter long-wing trend in the population. In *G. asper* these trends appear to be reversed.

2. While attempts to copy this seasonal determination artificially with *G. lacustris* were unsuccessful, a correlation between the polymorphic ratio and light and temperature was found in *G. asper*.

3. The results of breeding experiments on *G. lacustris* and *G. asper*, while supporting the monohybrid theory of Poisson (1924), demonstrate the influence of environmental factors.

4. Progeny ratios suggest the inviability of the short-wing homozygote, and this coupled with the disadvantage of flightlessness presumably constitutes the main check to the spread of the dominant short-wing gene through the population.

5. Possible selective advantages of the short-wing form appear to be its larger leg muscles and thus greater skating ability, and its shorter developmental life.

6. A brief examination of alary polymorphism in other insect groups and of *Drosophila* mutants, show that similar kinds of wing variation occur.

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THE SEPARATION OF MOLLUSCS FROM WOODLAND LEAF-LITTER

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The method described in this paper is an efficient way of separating some molluscs from leaves, but it cannot by itself be used to estimate the population densities of these animals. It is much more satisfactory than either Økland's (1929) or Jacot's (1934) methods. All three use a sieve. Økland simply shook leaves on a sieve and collected the animals in the debris falling through. If done carefully and slowly this, as many amateurs know, will give many more small snails than will be seen by rummaging through the litter, but it is easy to show that many slugs at least are not shaken off. Jacot's method also fails to produce slugs. He dried the leaves until they powdered and then sifted them away. It seems unlikely that a proper distinction between live snails and dead shells could be made this way.

In my method, the sieve and leaves are immersed in water. The first intention was to try detergents and salts to loosen the molluscs from the leaves, but trials with plain water showed, as will be seen, that this was not necessary. The apparatus consists of a zinc cylinder, 9 in. high and 13½ in. in diameter, closed at the bottom end except for a pipe leading from it. A circular piece of perforated zinc stands on one-inch high legs at the bottom of the cylinder and supports a piece of cloth sewn on to a circular piece of wire, the wire having a diameter very slightly greater than that of the cylinder. The wire is forced into position on the stand and the rim of the cloth is sealed off with a strip of plasticene. This prevents the possible loss of animals round the edge of the cloth when the apparatus is drained. An ordinary garden sieve of 1 cm mesh is wedged into the top of the cylinder, about ½ cu. ft of leaves is placed on the sieve and the whole is filled with water. For 15 min the leaves are stirred so that they float separately from each other, while water is run in at the top and out at the bottom. The molluscs fall through the sieve on to the cloth. The apparatus is then drained and the cloth searched.

The larger slugs and snails could be picked out quite easily, but many of the smaller ones are hidden under fragments of leaf that have fallen through, so the cloth must be searched with a binocular microscope; magnification ×6 is sufficient. This is done on a stand which consists of a circular piece of painted plywood rather larger than the cloth. The stand is mounted on an axle so that it can be rotated, and the lower end of the axle is attached to a frame with wheels which run on a short straight track, so that the stand can be moved from side to side. This system allows the cloth to be searched in a series of diminishing concentric circles. Even with freshly fallen leaves, which give the least debris, this can take 30 min, so that the sorting of one sample by this method can take at least an hour.

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The efficiency of the method was tested by examining each leaf under a binocular microscope in several samples that had been sieved in the apparatus. This is an exceedingly long and tedious process, but twelve samples were examined in this way, four from Cotswold beech litter collected in November 1952, the other eight from Wytham Wood, Berkshire. Of these eight, four were of predominantly hazel litter from Woodcroft Copse, collected in October 1952, and the other four were of beech litter, two from Plantation in October 1952, two from Brogdens Belt in January 1953. The Woodcroft and Plantation samples were each of 0·5 m², the other six only 0·25 m² as the larger sample gave rather too many leaves to be handled easily in the apparatus. There is no point in listing here all the animals caught in these samples, but some idea of the commonness of snails can be got from the lists of the biggest catches from both hazel and beech. These are, for hazel: *Carychium tridentatum* (Risso) 5, *Acanthinula aculeata* (Müller) 1, *Discus rotundatus* (Müller) 7, *Arion subfuscus* (Draparnaud) 5, *Euconulus fulvus* (Müller) 2, *Vitrea crystallina* (Müller) 6, *Oxychilus cellarius* (Müller) 7, *Retinella radiatula* (Alder) 2, and for the beech, one of the Plantation samples: *Carychium tridentatum* 28, *Cochlicopa lubrica* (Müller) 1, *Columella edentula* (Draparnaud) 1, *Acanthinula aculeata* 1, *Ena obscura* (Müller) 3, *Discus rotundatus* 5, *Vitrea crystallina* 3. Those figures include only the live animals. As judged by this series of tests, the apparatus is perfect; no live snail small enough to pass through all the meshes of the sieve was found in the leaves after sieving. For instance, in one of the Cotswold samples, the only molluscs that were sieved out were three *Vitrina pellucida* (Müller). Searching the leaves produced one more of the same species. A trial soon showed that all four snails could easily fail to fall through the sieve. In one of the Brogden Belt samples an adult *Carychium tridentatum* and an immature *Punctum pygmaeum* (Draparnaud) were found in the leaves. These were both dead and the mouths of the shells were blocked with dirt, so that the shells floated. This sample emphasizes the value of the method in finding very small snails, for four other immature but live *P. pygmaeum* were found, with maximum diameters ranging from 0·94 to 1·37 mm.

There are, however, three major disadvantages to the method. First, it is rather time-consuming. Second, it is almost useless with old leaves, for they break up very readily in water and fall through the sieve with the snails. Third, any soil collected with the leaves lengthens the time needed for searching the cloth; indeed not very much soil is needed to make the search almost impossible, especially for such species as *Acanthinula aculeata*. This last objection is serious. Not only is it almost impossible to collect leaves without some soil, but, more important, many, if not all, species burrow into the top soil, so that the leaves have only a proportion of the population. There is also a less serious disadvantage in that large species cannot pass through the sieve, but these species are mostly too rare to be sampled with small quadrats.

An attempt was made, without success, to overcome the difficulty caused by soil by placing samples in an upwards flowing column of water. This method has been used successfully to separate mites and collembola from sand grains

(Macfadyen, personal communication) but failed for snails because the snails and many of the small rocky fragments were all left in the heaviest fraction. The mud removed did not allow the molluscs to be found easily. For a method of this sort to be any use a large amount of soil would have to be sorted. This is stressed by some observations on young *Arion ater* (L.). In 1954 several clutches of eggs were placed in jars with about 4 in. of soil. On hatching, every one of several hundred slugs buried itself, and many of them dug right down to the bottom of the jars. As they grew older more and more took to living on the surface, but even so many half-grown slugs, the proportion varying considerably from jar to jar, spent their days underground, coming to the surface to feed at night.

Sieving in water then is a reliable method for separating small molluscs from undecayed leaves, but for larger species, and for all species living in soil and rotted leaves other methods are needed.

SUMMARY

1. A method is described of separating molluscs from woodland leaf-litter by sieving the leaves under water.

2. Apparently all live molluscs that can fall through the sieve do.

3. The method is time consuming, at least 1 hour is needed for each sample. If too much soil is included in the sample the method cannot be used.

4. Because woodland molluscs live both in the soil and in the leaf litter, this method cannot, by itself, give estimates of population density.

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REVIEWS

FISH POPULATION DYNAMICS

R. J. H. Beverton & S. J. Holt (1957). *On the dynamics of exploited fish populations.* (*Fish. Invest.* (2) **19.**) Pp. 533; 155 text-figures. London: H.M.S.O. Price £6 6*s*.

Let it be said at the outset that there is no doubt that this is an important book and is already well on the way to being the bible of fishery biologists the world over. It is one of the difficulties of ecology that much of its fundamental advance is made in specialized and applied fields whose literature is often neglected by those working in other fields of ecology and even by general ecologists. Fishery biologists have always been in the forefront of those interested in population dynamics and the study of populations and communities in quantitative and general terms—which is, after all, the real ecology. This is, perhaps, because fishery biology deals with large populations of a few major species dispersed over wide areas of similar habitat, and also because in few other fields of ecology is research so closely bound up with a large-scale industry. Rarely do other ecologists have the responsibilities and the rewards of having their forecasts and theories tested on so grand a scale. Thus, while at the same time dealing with problems that are basic to population ecology in general, it must be remembered that this book discusses these problems in the context of marine fisheries and moreover with the primary aim of producing practical advice for the regulation of one such fishery—the demersal fishery in the North Sea. Much of the discussion is therefore specific to fish and fisheries and has the limitations imposed by the unusual features of fish. Fish are very plastic in size and usually mature long before they reach their maximum size, so that their growth and ecological factors affecting it, such as population density, are of much greater importance than with many other animals. Most fish have a high fecundity and high, though variable, larval mortality, and a long adult life of continuous growth and low natural mortality is characteristic of many of the commercial fish species. The efficient regulation of marine fisheries is largely the problem of catching each year-class of fish at its most profitable age or size. The problem of providing for an adequate number of future recruits by regulation of the spawning population does not appear to be important, though the density relationships of larval survival are as yet virtually unknown. The problem of efficient fishing is therefore fundamentally a simple one, but one that involves a good understanding of both the growth and mortality aspects of fish population dynamics.

Beverton and Holt base their investigations on previous attempts to produce a theory of fishing, but they are far too modest when they say that they have done no more than underline and codify the conclusions of their predecessors. They have analysed the theoretical background much more thoroughly, have used a more realistic growth formula and above all have produced a more comprehensive model, or series of models, that take into account all the possible factors that are likely to be important. One of their more significant contributions is their linking of the minimum age or size at which fish are caught with the intensity of the fishing mortality. Thus sound fishery regulation should combine both mesh regulation and control of the amount of fishing. The importance of economic as well as biological factors is stressed and the authors' main conclusion on the North Sea fisheries is that while there is little prospect of a much greater total yield, such a yield could be obtained with about half the fishing effort and thus not much

more than half the cost. This book, therefore, paves a good stretch of a straight way from theoretical ecology to the price of fish and chips.

How relevant is the book, however, to ecologists who are not fishery biologists? The answer is, a good deal, but unfortunately most of the relevant items are scattered throughout the book and must be looked for amongst much that is of only fishery interest. The whole idea of an exploited population is, of course, relevant to the exploitation not only of fish populations or game bird or mammal populations by man, but also to a limited extent of any prey by any predator. Among the more important parts of the book of general interest are the elaborations of the simple theory in Part II where, among other things, both the possible relationships between numbers of spawners and resultant young fish, and the effects of population density on grazing and growth are discussed. Part III is devoted to the estimation of population parameters and contains many items that should be of use to workers in other fields. The estimation of mortality rates from age analyses, catch statistics and marking experiments is given full and in several places, original, treatment. Spatial variation in distribution, dispersion and migration are all discussed, often at considerable length, though on an almost entirely theoretical basis. The last part of the book develops the theories in application to North Sea fisheries and contains less of basic ecological interest. I think that my main disappointment with this book is that so much of general ecological value will inevitably lie shrouded from non-fishery ecologists by the material of solely fishery interest. Perhaps the authors might be persuaded and allowed to write a general book on population dynamics? This present book and its broad bibliography are good indications that such an effort would be well worth while.

Another discouragement to many readers will be the size, weight and cost of the book (though it is good value for these days), and the mathematical nature of much of the text. It is a theoretical work, based largely on mathematical deductive reasoning and using the language of simple algebra and calculus. Beverton and Holt, however, do base their models on actual data where available, and unlike many previous theories which fail through their limited resemblance to reality, theirs are rarely extrapolated far beyond the limits of observation and combine to a remarkably successful degree inductive description with deductive reasoning. Although much of the book is clearly written in plain language, and few readers will need to concern themselves with the algebraic steps in the derivation of the formulae, it is not easy reading for those many to whom any mathematical symbol is anathema. Whether we like it or not, however, this book is another demonstration that it is becoming increasingly difficult to make fundamental contributions to ecology without invoking the aid of at least some mathematics. The indices, bibliography and appendices of tables are good and helpful. There are also a number of figures, but in some places the explanation could have been made a bit shorter and clearer with the aid of a few more graphs. The printing and production are of high quality and I found remarkably few errors or misprints, but need the government publishers really have taken three and a half years after the completion of the manuscript to print and publish the book? Many of the individual passages and sections will doubtless give rise to argument and criticism. For example, not all will agree that the von Bertalanffy growth formula is satisfactory for all fish—though it certainly seems to for the authors' data. Similarly, the rather theoretical section on movements appears to use a lot of mathematics for the results it produces. The provocative nature of this work, however, will be one of its great virtues; it points clearly to those fields in which our ignorance is greatest and to those types of raw data that are most worth while to try to collect.

In conclusion I would recommend that all fishery biologists should read and if possible own this book. All ecological libraries should possess a copy and anyone working in population dynamics study much of it. Most ecologists would be stimulated by parts of

the book, if only for its convincing demonstration that there is an important place in ecology for thorough deductive theorizing, and heartening indication that such theories are already sound enough for large-scale practical application.

E. D. LE CREN

THE ECOLOGY OF COMMUNITIES

Janos Balogh (1958). *Lebensgemeinschaften der Landtiere: Ihre Erforschung unter Besonderer Berücksichtigung der Zoozönologischen Arbeitsmethoden.* (Zweite verbesserte und erweiterte ausgabe des 1953 erschienenen werkes 'Grundzüge der Zoozönologie'). Pp. xi+560. Budapest: Akademiai Kiado. (No price given.)

This book will probably be read for three different reasons; firstly as a thoughtful analysis and appraisal of the concepts of Synecology (Biozönologie) based on comparisons of the attitudes and vocabularies of the different world schools, secondly as a methodical resumé of methods for collecting, enumerating and handling terrestrial animals of all taxonomic groups, and thirdly as a short account of the work done recently in Budapest by this important group of workers in soil biology and productivity studies. In each of these fields, Dr Balogh has much to contribute.

The first part is a logical treatment of what is meant by a community (Biozönose) and related terms such as habitat, biotope, ecosystem and how they are studied. The ideas and systems of terminology of the European and Anglo-Saxon groups of ecologists are compared throughout and prove to have much more in common than many of us realize. Balogh shows that while the first group often think they are avoiding jargon by using everyday words, these are often used in special senses which may correspond closely with continental terminology. On the whole, however, there has been a gradual drift over the past 30 years in the meanings of terms, so that, for instance, Gam's 'Lebensformtypen' and Elton's 'Niches' which were once practically synonymous, have now acquired morphological and functional undertones respectively and are no longer compatible; this results in the final contradication of the 'habitat niche' of American authors. Balogh discusses rival views on the criteria of a community, the reasons for and against studying communities, the reality of edge effects and other topics, but he does not hesitate to advocate his own views, which are largely those of the Anglo-Saxon ecologists. For this reason, the main value of this section to the British reader will probably be the clear explanations of terms such as 'Konnex', 'Isozönose', 'Biochorion' and so on, whose definitions are so often taken for granted by those who use the words regularly. It is also most illuminating to find for instance Elton's 'interspersion' concept, Elton and Miller's habitat classification and their 'centres of action' idea related to the works of Tischler and others, and illustrated with examples from the experience of a different author.

The next part of the book is concerned with production biology and it benefits from first-hand experience in this field. The scheme is close to that now current in this country (which is the more remarkable because Odum's publications are too recent for inclusion). The bias is an essential empirical one, the main theme being that it is only by studying energy flow that we can hope to distinguish the more significant links in a complex food web. (The importance, however, of less active 'key' organisms is fully appreciated.) An interesting phenomenon discussed in some detail is the production of excess biomass by rapidly breeding herbivores (aphids, caterpillars) which act as a kind of energy store and may both smooth out and make more efficient the exploitation of plant food.

Although some of the topics discussed in these first sections are similar to those treated by Tischler (see review in *J. Anim. Ecol.* **26**, 213-14), and parts such as that which is concerned with cultivated land and other man-made environments are directly based on

Tischler's book, there is not in practice much common ground because Balogh adheres closely to a discussion of the properties of the community while Tischler covers a wider range, including climatic and physical factors and population dynamics. This is a subject which Balogh hardly mentions, while his section on production biology is much more extensive. The later sections of the book have almost nothing in common with Tischler's book which is based on a zoogeographical study of habitat factors, while Balogh is concerned with methods of studying terrestrial communities.

Part III covers methods of analysis and delimitation of communities on fairly familiar lines: numbers, biomass and activity; abundance, dominance and constancy and the trellis diagram; followed by the measurement of dispersion, the species/area curve and related topics. Nowhere else, however, can such a complete treatment of these topics be found inside a single set of covers. The final sections cover working methods for invertebrates, supplemented by special appendices on vertebrates by F. J. Turček and on the fauna of cultivated soils by Heydemann of Kiel. After much practical advice on general problems (*e.g.* choice of site, the appropriate contexts of qualitative and quantitative sampling methods, night work, methods of mapping distribution, counting, trapping and methods for special microhabitats) there are separate sections on each of the main groups of invertebrates, with regard to field study, counting, extraction, culture methods and handling techniques. The scope of this part of the book is extremely wide and while the specialist cannot fail to benefit from reading 'his own' sections, their special value will surely be for the newcomer and the specialist who seeks wider knowledge in other sections. This review is more complete than any other known to the author. A good deal of attention is given to comparisons of extraction efficiencies, although the more statistical approach to sampling characteristic of current British work receives but scant attention. This may be regarded as a failing but the fact remains that efficiencies of enumeration techniques have not been widely determined and Balogh gives a useful reminder that enumeration for its own sake is often a waste of time.

This is a unique book, embodying much practical experience in a very readable form and well illustrated by clear line diagrams; it also represents the outlook of an important centre of ecological learning, and it is to be hoped that 'Die Lebensgemeinschaften der Landtiere' will become widely known and that it will lead to an extensive exchange of ideas in a field of science which is too much dissected by national boundaries.

A. MACFADYEN

ECOLOGICAL ESSAYS

F. S. Bodenheimer (1958). *Animal Ecology Today.* Pp. 276; 41 text-figures. Den Haag: Junk (*Monographiae biologicae*, no. VI). Price *Fl.* 28.00.

This book is based on Bodenheimer's very stimulating book *Problems of Animal Ecology* (1938). The author's wide experience of different types of ecological studies enables him to avoid the extremes seen in some other recent texts, and gives him a reasonably balanced viewpoint.

The first chapter on 'physiological and ecological life tables' has been little altered from the earlier book, but the second, on 'the life history and its ecological interpretation' has been partly rewritten, and a third of the references are to papers published since 1938. The chapter considers the special problems of multivoltine species in relation to climatic factors, and leads up to a complex calculation of the 'ecological bonitation' of the fruit fly *Ceratitis capitata*. This is closely akin to Chapman's 'biotic potential', and the two conceptions have similar limitations. The rapidly growing topic of 'sense ecology and behaviour', might with profit have been expanded beyond the three pages devoted to it.

The third chapter, an 'approach to an analysis of some animal populations', retains a curtailed section on *Drosophila* from the earlier book and has new sections on aphids, the desert locust, malaria, voles and the muskrat. Errington's ideas on predation and his stress on compensation have evidently had considerable influence on the author, and Errington's name appears with those of Snelford, Hesse and Nicholson as one of the pioneers of ecology to whom the book is dedicated.

Long quotations introduce in Chapter 4 the vexed questions of biological equilibrium in nature, and biological control. Bodenheimer's views have changed significantly since the earlier book, and he no longer overstresses the significance of climatic factors. Unfortunately the different meanings of the word 'control' are not clarified in the quotations given, and a synthesis of the divergent views escapes him. 'The mathematical and experimental approach' introduces the ideas of Lotka, Volterra, Gause, Utida and Nicholson, but different usages of the word 'oscillation' and different methods of graphical presentation receive no comment. It is confusing to compare graphs of population changes in which each point represents the total number of animals in a generation (Utida) with Nicholson's superficially similar *Lucilia* 'oscillations' where each point is a weekly count of long-lived flies, and each 'cycle' could perhaps represent a single generation of flies. Neither Nicholson nor Bodenheimer consider this possibility, nor the alternative, that the numbers are to be intepreted in the light of the theoretical curves of Ricker (which are given in detail a few pages further on, and have been applied by him to fish populations). On this model overcrowding has such a severe effect on the numbers of the next generation that generations of large and small numbers of individuals alternate with each other. The mechanism of this kind of population instability is so different from that of the predator-prey oscillation that is a pity that the same word has been used for both.

The author is not entirely clear on the important subject of density-dependent factors. On p. 125 they are stated to cause cycles. Yet predator-prey cycles involve the very different delayed density-dependent relationship. Three pages later Bodenheimer approves the extended use of the term density-dependent factor to cover inverse factors, which is quite contrary to the original definition of the term. He does not point out that since inverse factors are density disturbing in their influence, this is not in accordance with his earlier statement.

This chapter would have been much easier to follow if some of the definitions given at the beginning of Chapter 5 had come much sooner, for here Bodenheimer rightly contends that 'most of the controversies and misunderstandings are caused by ambiguous definitions, misunderstandings concerning the same term, or translation of philosophical concepts into nature, where they have no place'.

The penultimate chapter discusses environment and heredity, and about 14% of the references are new. The final chapter, on human ecology, is entirely new, and presents a gloomy picture of man's reckless and destructive exploitation of the world in which we live.

The book is well printed, on good paper, and is reasonably free from typographical errors, although some errors in the mathematical formulae and of spelling may bother the reader; some graphs and tables would have been improved with fuller explanatory legends. Considering how much of the book remains unchanged from 20 years ago, it reads with remarkable freshness; its scope and emphasis remain quite individual. It has the merits of reasonable brevity, yet the topics treated are considered in sufficient detail for the methods used in handling the numerical information to be clear. Many will find the book a useful stimulus.

G. C. VARLEY

MARINE ECOLOGY

Joel W. Hedgpeth (Editor) (**1957**). *Treatise on Marine Ecology and Paleoecology*, Vol. I, *Ecology*. Pp. viii + 1296; 27 plates; 297 text-figures. New York: The Geological Society of America (Memoir 67). Price $12.50.

This is the first volume of the great treatise produced by the American Geological Society primarily intended for geologists and palaeontologists, the second volume of which was reviewed in the November 1958 number of this Journal. Volume II was published in March 1957, and Volume I in the following December.

Following the dictum of Sir Charles Lyell that 'the present is the key to the past', the Research Council of the National Academy of Sciences, on the instigation of Dr T. Wayland Vaughan, formed a subcommittee in 1940 under the chairmanship of Harry S. Ladd to correlate researches on the ecology of marine organisms; they issued a preliminary report in 1941. In 1942 they were raised to a full committee, the terms of reference being 'Marine ecology as related to paleontology', and they issued a second report at the end of that year suggesting that a special treatise should be prepared later on this subject. The activities of the committee were seriously curtailed by the Second World War, but in 1946 the 6th annual report contained an outline of this treatise; then in 1947 Gordon Gunter was elected Vice-chairman for biology, Kenneth E. Lohmann for geology and Roger Revelle for oceanography, and subsequently concrete plans were made for the completion of the work. The committe at this time numbered nineteen, all well known for their work in this field, and the help of nearly a hundred specialists was obtained. The result, published in 1957, is a very comprehensive survey of marine ecology, even disregarding its particular purpose. In a way, it is unfortunate that such a work should stem from a Geological Society, since there is a chance that biologists will be unaware of the existence of this first volume; it is such a noble work that it should certainly find a place on the shelves of every biological library.

The editor of Volume I, Joel W. Hedgpeth, has clearly been energetic in co-ordinating the various chapters, and in exhorting the authorities concerned to reduce to a minimum the specialized terminologies; he has produced four introductory chapters on the history and concepts of marine ecology, the classification of environments and (with Gunnar Thorson and Gordon Gunter) on methods of sampling and observation, as well as writing in the main body the chapters on Marine Biogeography and Sandy Beaches, and contributing to that on Estuaries and Lagoons.

In his history of the subject (Introduction), Hedgpeth traces the story from Wahlenberg's early efforts through d'Orbigny, Forbes, Michael Sars, Lovén and Müller as pioneers in their own countries, leading to the great oceanographic *Challenger* Expedition of 1872-6. He shows how Victorian England caught the craze for holiday classes in seashore study; how the first government commission on fisheries' problems was set up in the 1860s by Britain, followed by others in Germany and America inspired by such men as Möbius and Verrill; and how the use of diving gear, measured grabs and quadrat methods led to quantitative studies by such men as Petersen and Gislèn. He gives prominence in the history of marine ecology to the foundation of the Plymouth Marine Laboratory, catering as it does for academic studies in physiology and ecology as well as in fisheries' problems. His chapter on the Concepts of Marine Ecology contains a useful summary of the organization of ecosystems, stressing the interaction not only of every organic and physical component in one particular system but also of one system with another: the interdependencies of many major marine communities are more pronounced than they are on land. Good quantitative studies, he points out, are few, and our knowledge of the trophic structure and dynamic relationships of the sea is meagre in consequence. The author apologizes in a postscript (p. 48) for the absence of any section on statistical

methods in marine research, offering the excuse that a competent authority could not be found. This, as he admits, is a most serious and unfortunate omission, but his warning about the indiscriminate use of stereotyped methods in inappropriate circumstances by ecologists is timely.

Following the first five introductory chapters on the broad principles and practice of the subject are seven chapters on the physics and chemistry of the sea, all remarkably complete summaries with full bibliographies. Some of them contain most useful asides on related controversial subjects such as that on the possible brackish habitat of the original vertebrates in Pearse and Gunter's chapter on Salinity; unfortunately this review was completed before some of the recent suggestions of a marine origin had appeared. Next comes Hedgpeth's contribution on Marine Biogeography in which he reviews the main aspects of this vast subject which have so far been synthesized, laying the main emphasis on the factor of temperature. After a short but excellent chapter on the quantitative study of suspended organic matter by Fox come three sections on the interrelations of organisms, followed by the main contributions which this book has to offer the biologist, namely, eight chapters on various habitats, such as the plankton, bottom communities (an excellent, well-illustrated review by Gunnar Thorson), rocky, sandy and estuarine shores, coral reefs, submarine canyons and abyssal depths. All these are exhaustive. There follows now a series of special accounts on particular enclosed, or nearly enclosed, seas, the Baltic, Caspian and Aral seas, the Black Sea and the Sea of Azov, which, by virtue of their isolation from the oceans, have been used as gigantic aquaria. Casper's and Zenkevich's accounts are particularly useful since they review the mass of Russian literature which has emerged since about 1923 on the Black Sea and the Caspian. Lastly, in the main body of the book, Corringa contributes an account of Lunar Periodicity and Mrs Brongersma-Sanders gives a very full account of mass mortality in the sea.

The last 200 or so pages contain annotated bibliographies of ecological works, starting with general books and papers, and works dealing with fouling and boring organisms, and finally sections on every major marine plant and animal group. These sections, together with the bibliographies of specialist chapters, make the whole work a most valuable volume to grace any biological library.

The whole concept of producing this two-volume treatise, lasting as it has 17 years, should earn the full praise of every ecologist; it is a tremendous success, and when biologists have discovered it, there is no doubt that its pages will be well thumbed for many years.

DAVID NICHOLS

ECOLOGICAL EXPEDITION

Guy Mountfort (1958). *Portrait of a Wilderness: the story of the Coto Doñana Expeditions.* Pp. 240; 60 plates (8 in colour). London: Hutchinson. Price 30*s*.

Anyone who is a keen ornithologist will already have seen reviews of this book in ornithological journals, so that my remarks are intended more for those who do not suffer from what the author refers to as 'ornithomania'. It is the story of three ornithological expeditions to the Coto Doñana in 1952, 1956 and 1957, and as such it is a book primarily about birds, but containing much of more general interest about a most fascinating corner of south-west Spain.

To my mind the most valuable chapter of the book is the last one, which is contributed by E. M. Nicholson as joint ecologist to the last expedition. This describes clearly the basic ecology of the Coto Doñana, whose present shape and character are the result of a very special ecological history and geography. Without some understanding of this, the

reasons for the amazingly rich bird life described in the book are not apparent; and it is indeed a pity that this chapter did not come as an introduction at the beginning, so that the reader could fit the rather disjointed accounts of other chapters into a general ecological pattern. Admittedly the book was written for the general public (it is in fact recommended by the Book Society), but this last chapter is no more difficult to assimilate than, for example, the account of six species of lark in Chapter 5.

The Coto Doñana lies just north of the present entry of the Guadalquivir into the sea, on part of the former delta of this river, against which sand has been piled up by south-west winds and coastal currents to produce a great sand belt several miles broad. Here is exhibited a complete series of dune evolution, from bare sand to both stabilized and mobile dune ridges, which attain heights of over 300 ft; and between the ridges are flat damp depressions with woods of introduced stone pines. Further inland the area of unstable dunes and pine woods passes into a stabilized and flattened sandy tableland at about 50 ft above sea level. Here there is open scrubland, park-like areas of cork oaks and thickets of tree-heath and bramble, while separating dunes and tableland is a line of freshwater lagoons. Eastwards the semi-arid plateau changes into the swampy and low lying *marismas*, where sand ceases to overlay the silt of the delta, a vast region of marsh, with mainly saline water, which is flooded annually for about 5 months in winter. There is thus in the course of only 6 miles from the sea an extraordinary diversity of natural habitats, which is partly responsible for the wealth of animal life found here. The wet *marismas* attract vast flocks of waterfowl in winter and hold a fauna capable of supporting a wide variety of other birds, especially birds of prey, which breed on the drier habitats. Mr Nicholson points out that the Coto is also placed on the hinge between Europe and Africa, thus drawing on a very wide range of species, and it has not suffered the impoverishment of successive Ice Ages. All these factors, however, would have availed nothing if the owners for many generations had not also cared for and protected the area from the damage of modern economic exploitation.

The first chapter gives an account of the history of ownership and then follow chapters describing the personnel and something of the work of the three expeditions. Photography of birds which are rare or unknown in Britain formed an important part of the programme, and the book is indeed profusely illustrated with wonderful studies by Eric Hosking, mostly in monochrome but some in colour. Material was also collected for the fine colour film 'Wild Spain', which many people may have seen. Most of the subsequent chapters are concerned with birds, which are described either as groups or under habitats. There are accounts of hide building and the photographing of birds at their nests, but there is also much to interest those who are not particularly keen on photography, and above all the richness of of the avifauna is vividly portrayed. I was excited to read a modern account of the great bustard, of the flamingoes which no longer breed perhaps because of the decreasing salinity of the *marismas*, of the tunnelling of bee-eaters in flat ground and of the spread of the cattle egret. There is a chapter on the wild animals of the Coto, which includes information about wild boar and lynx, and a short one on the plant and insect life which I found less satisfactory. It might surely have been better to take an experienced entomologist on the last expedition, instead of the author collecting some 300 species of insects for the British Museum. Finally there are appendices listing the birds of the Coto Doñana, and the amphibia, reptiles and mammals of Andalucía.

A book about expeditions of this sort should contain good maps, but there is only one rather inadequate map at the front, which is repeated at the back of the book. It is irritating to keep on reading the names of places which there is no means of relating to anywhere else, and I also felt the need of a sketch map to show exactly where the Coto Doñana lies. It is perhaps pertinent to mention also that a fuller account of the ecology of the Coto, by Valverde, has been published in *British Birds* (1958, **51,** 1-23) and a comparison of the region with the Camargue by Nicholson *et al.* (1957, **50,** 497-519). The

habitat photographs illustrating these two papers are excellent and a few more of these in the book, at the expense of a few birds, would have made all the difference by helping the reader to visualize the country.

Perhaps the main value of Guy Mountfort's book, and it is a considerable one which Viscount Alanbrooke mentions in his introduction, is that it must have drawn the attention of a great many people to the existence of the Coto Doñana as one of the very few great sanctuaries of wild life remaining in Europe. While a year or two ago only a handful of people in this country might have protested if its preservation had been threatened, now surely there will be a large body of opinion on both sides of the Atlantic. There is, however, the danger, which the author appreciates, that a book such as this may stimulate readers to go there themselves, and in a laudable last page he points out that it is private property, which the owners wish to keep as a strict sanctuary, and that most of its wild life can also be seen in other more accessible parts of Andalucía.

P. F. HOLMES

FISH PHYSIOLOGY

Margaret E. Brown (Editor) (**1957**). *The Physiology of Fishes*, Vol. II, *Behaviour*. Pp. xi + 526; numerous text-figures. New York: Academic Press. Price $14.00.

This volume completes *The Physiology of Fishes*. While Volume I dealt with subjects grouped under the general heading of metabolism, this second volume is concerned with the physiological aspects of fish behaviour. The following subjects are discussed: the Nervous System by E. G. Healey, the Eye by J. R. Brett, the Acoustico-lateralis system by O. Lowenstein, the Olfactory and Gustatory Senses by A. D. Hasler, Conditioning Responses by H. O. Bull, Ethological Analysis of Fish Behaviour by G. P. Baerends, Reproductive and Parental Behaviour by L. R. Aronson, The Swimbladder by F. R. Harden Jones, Electric Organs by R. D. Keynes, the Luminous Organs by E. Newton Harvey, Pigments by D. L. Fox, Colour Changes by J. M. Odiorne, Water Quality Requirements of fishes and effects of toxic substances by P. Doudoroff, and Physiological Genetics by M. Gordon. As can be judged by this subject list the field of physiological aspects of behaviour is well covered, and the authors are to be congratulated on the extensive survey which each gives of his particular subject. Like Volume I this is an excellent reference book, and together they give very extensive coverage of the literature. In doing this the authors have rendered a great service to all people interested in fish.

Although much more readable than Volume I, like it this volume lacks a critical appreciation of the literature. One wonders if this review approach is the result of a deliberate editorial policy; whatever the reason, the result is an unfortunate one, for once an observation has been recorded in a book of this kind it tends to become an accepted fact. Apart from its obvious interest to fish physiologists this work should prove of great value to fish ecologists and in particular those who are concerned with pollution problems; indeed the following quotation from the chapter on Water Quality Requirements: 'A distinction must be made between tolerable environmental conditions determined experimentally in the laboratory and those conditions under which fish can be expected to occur and thrive in nature', could with advantage be a slogan for all people interested in this aspect of pollution. Perhaps now that we have, collected together in these two volumes, a survey of the vast majority of the literature, we can hope for a critical survey of this comparatively new field of study.

D. R. SWIFT

NAMES OF VERTEBRATES

R. D. Macleod (1956). *Key to the Names of British Fishes, Mammals, Amphibians and Reptiles.* Pp. viii+71. London: Pitman. Price 12*s.* 6*d.*

Continuing his key to the names of British birds, Mr Macleod has now turned to the remaining vertebrates; he has also compiled a book of the names of British plants. For the fishes and mammals he has used the British Museum lists: the amphibians and reptiles have been taken from the late Malcolm Smith's volume in the New Naturalist Series.

The scientific names are considered in the first part of the book, the common names in the second. The meaning and derivation of these names are given, as far as they are known, but before this comes an introductory section giving the purpose and plan of the book, some grammatical principles and some account of the origins of scientific and common names.

A book of this kind is almost bound to be incomplete. Species of the genera *Myctophum, Lampanyctus, Lampadena, Diaphus*, etc., could have been given the common name of 'lantern fishes'. Similarly, those of the genera *Lionurus, Coryphaenoides*, etc., can be called 'rat-tails' or 'grenadiers'. *Katsuwonus pelamis* is better known as the 'skipjack' rather than 'bonito'. There are oversights on pages 1 and 11, the 'mackerel' being called *Clupea harengus* and *Leuciscus* 'hake'.

However, this book will surely be welcomed by both naturalist and specialist. In his introduction, Mr Macleod remarks that the advantages of scientific names are international and systematic, while a knowledge of their derivation is a useful aid to memory. Common names can lead to confusion but have their intriguing aspects. From 'ablet' to 'wriggle', 'badger' to 'whittret' and 'adder' to 'viper' there are words for poets as well as naturalists. In bringing these and their counterparts together, Mr Macleod has given us a pleasing addition to the semantics of British natural history.

N. B. MARSHALL

ARACHNIDS AND OTHERS

J. L. Cloudsley-Thompson (1958). *Spiders, Scorpions, Centipedes and Mites.* Pp. xiv+228; 16 plates; 40 text-figures. London; Pergamon. Price 50*s.*

The title of this book is somewhat misleading; its eleven chapters deal with woodlice, millipedes, centipedes, other myriopods, scorpions, solifugids, false-scorpions, whip-scorpions and others, harvest spiders, spiders, mites and ticks. The chapters are subdivided into sections on classification and distribution, general behaviour, food and feeding habits, enemies, reproduction and life cycle, a choice of topics which indicates the author's intention of interesting natural history workers and providing them with a guide to the taxonomic literature—a guide which, however, is more economically provided by Smart and Taylor's *Bibliography of Key Works for the Identification of the British Fauna and Flora.*

The book has some of the qualities of the older natural histories: a love of facts for their own sake; an entertaining discursiveness unhampered by the systematic divisions of the chapters; a tendency towards anthropomorphism (some hunting spiders 'spend the night under any suitable rock or stone they come across'; and mites led 'a blameless existence' before becoming parasitic); an occasional quaintness of expression ('in the silence of the night, the desert solifugae race about, conduct their amours and glut themselves on innumerable insects to supply their requirements during the winter sleep'). However, Dr Cloudsley-Thompson has set himself the difficult task of combining the

diversity of a natural history with the integrating principles of zoological science, and reference is made to such problems of current interest as the properties of arthropod cuticle, diurnal rhythm, arachnid proprioception, and the role of density-dependent factors in population control. The treatment of these matters is necessarily brief—for instance density-dependent factors in population control occupies a paragraph in the section on the enemies of harvest-spiders. This is likely to prove too brief for the natural historian and too superficial for the academic zoologist. However, there is a short bibliography at the end of each chapter with references to some of the more detailed literature.

One outstanding quality pervades the book: its author's enthusiasm for the animals with which he deals and about which he possesses much first-hand knowledge. This will stimulate interest among natural historians and academic zoologists alike in groups of arthropods which have lain for too long under the shadow of the insects. The book is well produced, illustrated and indexed; and contains a useful glossary of the scientific terms used in the text.

D. A. PARRY

POPULAR ECOLOGY

Leslie Reid (1958). *Earth's Company.* Pp. xi+221; 12 plates; 8 text-figures. London: Murray. Price 25*s*.

The popular exposition of the ideas and theories of science is an even more difficult art than the presentation of scientific facts for general readers. The author of this book is therefore to be congratulated on his attempt at an original approach to the writing of a biological book, as *Earth's Company* is not just another catalogue of the more bizarre and striking facts of natural history, but a serious effort to present, with popular appeal, the basic ideas of animal ecology and related fields of biology. The book appears to have few factual inaccuracies, but there are some of those errors in emphasis that are usual with second-hand reporting. Real understanding may not be necessary for the popular exposition of fact but it is essential for the explanation of theory in a simple and stimulating manner; I did not feel that all the theories in this book had been thought about deeply or critically. *Earth's Company*'s weakness, however, lies in its style of presentation. This may be appreciated by some but I found it unsatisfactory and often irritating. Too many of the words are used to describe the processes of explanation, rather than that which is being explained, and too often an interesting topic is given considerable introduction and build-up and then left quite inadequately described. Although both purple passages and jargon are rare, some painted terminology, such as 'deadly predation', does occur. More straightforward description and thorough presentation of a few well-understood examples would have helped the book; as would also a more adequate and relevant set of illustrations. In spite of its shortcomings some may find in this book a stimulating introduction to the ideas of ecology; it certainly champions the ecological approach to popular biology.

E. D. LE CREN

LIMNOLOGICAL BIBLIOGRAPHY

Martin Scheele (1958). *50 Jahre Archiv für Hydrobiologie: eine Literatur-Analyse der Limnologie dargestellt an den Bänden 1 bis 50, 1906 bis 1955.* Pp. vi+175. Stuttgart: Schweizerbart. Price DM 36.00.

This index to the first fifty volumes of the *Archiv für Hydrobiologie* (excluding the supplementary volumes) is more than a simple index, since it sets out the results of a (Hollerith) punch-card analysis of the content of the 1385 papers published in these 50 years.

After a brief historical introduction, at the end of which the work is dedicated to Professor Thienemann on his 75th birthday, a series of twenty-eight tables set out the results of classifying the papers in a variety of ways. For example 20% of papers occupy 21-50, 20% 11-20, and 20% 6-10 pages; it is a little shocking to read that 80% of the papers have no summaries, and surprising to find that 53% have no text-figures; as many as 90% contain no detailed treatment of methods, while 83% deal with communities (Cönobiologie). An analysis by organ-systems shows such a wide scatter that no percentages are given, but the alimentary and urinogenital systems and the organs of attack and defence are the most popular. Of physico-chemical factors temperature (22%), hydrogen ions (12%) and oxygen (12%) have attracted most notice. European waters claim 56% of papers, followed by Asia (3·5%), Africa (3·2%), South America (2·4%) and North America (1·3%). The most favoured group of organisms is the Bacillariophyta (16%) followed by the Rotifera and the Phyllopoda (both 12%), and the Copepoda (11%); next come Diptera (9·8%), Arachnomorpha (7·8%) and fish and cyclostomes (7·7%), but all the insects together make up 27·2%.

The next part of the book consists of an index, arranged alphabetically by authors, of all the original papers (excluding book reviews, etc.) with their titles and page references; to each is attached a set of seven figures, which by a code indicate the paper's length, language and summary, and the numbers of plates, figures, tables and titles in the reference list; five more figures give the year and the paper's serial number in that year. This index of titles, which occupies 72 pages, is followed by a series of some 140 lists by subjects, occupying 78 pages. Each of these shows which papers deal with the subject in question, identifying them by the author's name and initials (arranged alphabetically) and the series of twelve figures describing the paper mentioned above. Thus to find the titles of all the papers published by an author is simple, and it is equally simple to find which authors have dealt with a given subject in what year and at what lengths, but to obtain their titles and page references one must refer back from the subject list to the index of titles.

The book is excellently produced and will be a valuable adjunct to a run of the fifty volumes of the journal.

H. C. GILSON

BOOKS RECEIVED

Die Biologie des Brackwassers by Adolf Remane & Carl Schlieper. (*Die Binnengewässer*, Vol. XXII). Stuttgart: Schweizerbart. 1958. Price DM 55.00.

Marine Ecology by Hilary B. Moore. New York: Wiley; London: Chapman & Hall. 1958. Price 76*s*.

A Study of Blackbirds by D. W. Snow. London: Allen & Unwin. 1958. Price 21*s*.

Living Resources of the Sea: opportunities for research and expansion by Lionel A. Walford. New York: Ronald. 1958. Price $6.00.

An Introduction to the Behaviour of Invertebrates by J. D. Carthy. London: Allen & Unwin. 1958. Price 45*s*.

Listening in the Dark: the acoustic orientation of bats and men by Donald R. Griffin. New Haven: Yale U.P.; London: Oxford U.P. 1958. Price 60*s*.

Seals, Sea Lions and Walruses: a review of the Pinnipedia by Victor B. Scheffer. Stanford U.P.; London: Oxford U.P. 1958. Price 30*s*.

The Story of Evolution by Sir Julian Huxley (illustrated). London: Rathbone Books. 1958. Price 17*s*. 6*d*.

Books on Agriculture and Horticulture. (M.A.F.F. Bulletin No. 78) London: H.M.S.O. Price 5*s*. 6*d*.

At the Farmer's Service. London: M.A.F.F. 1958. Gratis.

Investigations of Ring-Necked Pheasants in Illinois by Wm. B. Robertson, Jr. (*Tech. Bull. Ill. Dept. of Conservation, Div. Game Management,* No. 1) Springfield, Ill. 1958. (No price given.)

The Passage of Smolts and Kelts through Fish Passes. London: H.M.S.O. 1957. Price 1*s.*

Proceedings of the New Zealand Ecological Society. No. 5 (Dec. 1957). Wellington, P.O.B. 202. Price 7*s.* 6*d.*

Annales Biologici (*Tihany*) *Hungaricae Academiae Scientiarum.* Vol. XXV. Tihany. 1958.

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with assistance in selection and abstracting of J. A. Allen, J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, F.A.O., Fisheries Division, P. D. Gabbutt, N. A. Holme, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs. M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s*. 6*d*. per annum, post free (issued in May and November). Back numbers of the 'Notices of publications ... ' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s*. for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologists Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Barnes, H. (**1958**). The growth rate of *Verruca stroemia* (O. Müller). *J. Mar. Biol. Ass. U.K.* **37,** 427-433.

Compares the mean specific growth rate of the species at half its maximum size with those of other common barnacles.

Crisp, D. J. (**1958**). The spread of *Elminius modestus* Darwin in north-west Europe. *J. Mar. Biol. Ass. U.K.* **37,** 483-520.

A broad survey of the history and ecological effects of the invasion of Europe by this barnacle.

Forster, G. R. (**1958**). Underwater observations on the fauna of shallow rocky areas in the neighbourhood of Plymouth. *J. Mar. Biol. Ass. U.K.* **37,** 473-482.

Surveys the commoner sessile animals seen during dives near Plymouth, including three offshore reefs.

Gotto, R. V. (**1957**). The biology of a commensal copepod, *Ascidicola rosea* Thorell, in the ascidian *Corella parallelogramma* (Müller). *J. Mar. Biol. Ass. U.K.* **36,** 281-290.

Describes feeding and reproduction.

McCartan, L. (**1958**). The wreck of kittiwakes in early 1957. *Brit. Birds,* **51,** 253-266.

Over 900 kittiwakes were reported on the south and west coasts of England and Wales and the east coast of Ireland in January and February 1957. Mortality attributed to starvation was high. Such wrecks may result when a large flock in the North Atlantic occurs in the direct path of a storm.

McCartan, L. (**1958**). Mortality of kittiwakes during the breeding season. *Brit. Birds,* **51,** 267-268.

In one instance *Aspergillus fumigatus* caused heavy mortality among adult kittiwakes, in others the cause was not determined. Fledged juveniles sometimes die in large numbers, apparently from starvation.

McIntyre, A. D. (**1958**). The ecology of Scottish inshore fishing grounds. I. The bottom fauna of east coast grounds. *Scottish Home Dept., Mar. Res.* **1,** 1-24.

A first study of the fluctuations and productivity of the benthos in relation to fish feeding, made from grab surveys of three grounds off the east coast.

Mason, J. (**1957**). The age and growth of the scallop, *Pecten maximus* (L.), in Manx waters. *J. Mar. Biol. Ass. U.K.* **36,** 473-492.

Analysis by growth rings shows that growth ceases during winter. Possible causes are discussed.

Matthews, L. H. (**1958**). Calving time of grey seals. *Nature, Lond.* **182,** 1325-1326.

Grey seal pups have been recorded on the British coast for every month except February. Restricted calving periods may exist in different localities.

Morton, J. E., Boney, A. D. & Corner, E. D. S. (**1957**). The adaptations of *Lasaea rubra* (Montagu), a small intertidal lamellibranch. *J. Mar. Biol. Ass. U.K.* **36,** 383-405.

Field and laboratory studies on the adaptations of this mollusc particularly in relation to degree of submersion.

Parrish, B. B. & Craig, R. E. (**1957**). Recent changes in the North Sea herring fisheries. *Rapp. Cons. Explor. Mer.* **143,** 12-21.

Use of catch and effort statistics, size and age compositions and mortality rates in interpreting the state of the fishery. With an appendix on plankton indicator results by R. S. Glover and on temperature and salinity by Craig.

Shelbourne, J. E. (1957). The feeding and condition of plaice larvae in good and bad plankton patches. *J. Mar. Biol. Ass. U.K.* **36,** 539-552.

The problem is considered in relation to early mortalities among food fishes.

Southward, E. C. & Southward, A. J. (1958). The breeding of *Arenicola ecaudata* Johnston and *A. branchialis* Aud. & Edw. at Plymouth. *J. Mar. Biol. Ass. U.K.* **37,** 267-286.

Discusses breeding cycles, behaviour and development of these two lugworms.

(*b*) Fresh water

Brindle, A. (1958). Night activity of Trichoptera. *Ent. Mon. Mag.* **94,** 38-42.

Samples of Trichopteran imagines taken at night show that the activity curve may be unimodal or bimodal, and that flight types can be distinguished as dusk flight, night flight, and intermittent flight.

Brown, E. S. & Scudder, G. G. E. (1958). Notes on the rarer British species of aquatic and semi-aquatic Hemiptera: III. *Micronecta minutissima* (L.). *Entomologist,* **91,** 15-19.

This corixid is recorded for the first time from Northamptonshire, Oxfordshire and Hertfordshire, with descriptions of the habitats in the last two. Favourable conditions appear to be semi-stagnant or very slow-flowing water of neutral or slightly alkaline reaction, a rather muddy bottom, and thinly scattered submerged or floating vegetation. It is also known from Wiltshire, Essex and Eriskay; other published records probably refer to *M. poweri.*

Edwards, R. W. (1958). The effect of larvae of *Chironomus riparius* Meigen on the redox potentials of settled activated sludge. *Ann. Appl. Biol.* **46,** 457-464.

High populations of *Chironomus riparius* larvae in consolidated sewage sludge caused rises in pH values, an increase in the depth of the surface layer in which redox potential was high, and increased pH values in the overlying water.

Hanna, H. M. (1957). A study of the growth and feeding habits of the larvae of four species of caddis flies. *Proc. R. Ent. Soc. Lond.* (A), **32,** 139-146.

Describes the growth and feeding habits of *Limnephilus politus, L. marmoratus, Molanna angustata* and *Anabolia nervosa.*

Hinton, H. E. (1958). The pupa of the fly *Simulium* feeds and spins its own cocoon. *Ent. Mon. Mag.* **94,** 14-16.

The importance of pharate stages is emphasized with reference to the pupa of *Simulium* which carries out a variety of activities not normally associated with pupae.

Jackson, D. J. (1958). Observations on *Hydroporus ferrugineus* Steph. (Col. Dytiscidae), and some further evidence indicating incapacity for flight. *Ent. Gaz.* **9,** 55-59.

Notes on captive beetles suggest its incapacity for flight. Its distribution in springs and winterbournes suggests that it survives dry periods by retreating into subterranean waters.

Lansbury, I. (1957). Observations on the ecology of water-bugs (Hemiptera: Heteroptera) and their associated fauna and flora in south-east Kent. *Entomologist,* **90,** 161-177.

The numbers, habitat preferences and species associations of 22 water bugs collected in 22 ponds and dykes in Romney Marsh, the ecological characters of which are given, are discussed. Lists, with distribution notes, of the Coleoptera, Odonata, Gastropoda and plants present are included.

Mundie, J. H. (1957). The ecology of Chironomidae in storage reservoirs. *Trans. R. Ent. Soc. Lond.* **109,** 149-232.

A survey made of the Chironomidae of three reservoirs in Middlesex. The bulk of the data obtained by trapping emerging chironomids. Emergence estimates for named species show the depths at which the species occurred, the optimum depth, the number of generations per year at different depths, the date of emergence, the skewness and kurtosis of the distribution and the effect of increase in depth on the time of emergence. The distributions of the species are discussed in relation to their feeding habits and respiratory requirements. Differences between sites are discussed.

Reynoldson, T. B. (1958). Triclads and lake typology in northern Britain — qualitative aspects. *Verh. int. Ver. Limnol.* **13,** 320-330.

Discusses distribution of lake triclads in relation to calcium content and general habitat conditions in lakes. Contrasts are recorded with lakes in Sweden.

Reynoldson, T. B. (1958). The quantitative ecology of lake-dwelling triclads in northern Britain. *Oikos,* **9,** 94-138.

A broader and closer analysis of the author's data (*vide* Reynoldson, T. B., *supra*) with a summary of the taxonomy of the group and drawings and notes to aid field recognition of British species.

(*c*) Land

Ash, J. S. (1958). Partridges apparently affected by industrial contamination. *Brit. Birds,* **51,** 241-242.

An irritant such as carcinogen is suggested as the cause of deformity in the upper mandibles of two partridges shot near collieries in Yorkshire.

Blackith, R. E. & Roberts, M. I. (1957). Farbenpolymorphismus bei einigen Feldheuschrecken. *Zeitschr. Vererbungsl.* **89,** 328-337.

Analysis of sexual dimorphism, specific and colour polymorphism in acridians by measuring, classifying and combining into one measure ten morphometric characters. The results contradict Vavilov's rule.

Bone, Q. & Hardy, M. G. (1958). Some observations upon a polymorphic population of *Argynnis paphia* (L.) (Lep., Nymphalidae) in the New Forest. *Ent. Mon. Mag.* **94,** 114-119.

A population of the butterfly *Argynnis paphia* sampled in the New Forest showed a high proportion of the polymorphic form *valesina*. A full discussion of the possible factors affecting the frequency of the polymorphism is given.

Brown, S. C. S. (1958). Five species of ants (Hym., Formicidae) inhabiting the same nest. *Ent. Mon. Mag.* **94, 5.**

A colony of *Formica sanguinea* was noted which, in addition to its usual slave, had workers of three other species in the nest.

Cawthra, E. M. (1957). Some notes on *Grypidius equiseti* F. (Col.: Curculionidae) with a description of its larva. *Proc. R. Ent. Soc. Lond.* (A), **32,** 95-106.

Gives brief notes on distribution, habits, behaviour of adults, copulation, eggs and hatching, and larvae and development.

Dance, S. P. (1958). A note on *Helicodonta obvoluta* (Müller). *J. Conch.* **24,** 278.

A supplementary note to Beeston's paper (*J. Conch.* **16,** 31-36, 44-50) on the ecology of the very local snail *H. obvoluta*, drawing attention to its frequent association with dog's mercury (*Mercurialis perennis*), contrary to Beeston's statement that this snail is not found amongst this plant.

Davis, G. A. N., Frazer, J. F. D. & Tynan, A. M. (1958). Population numbers in a colony of *Lysandra bellargus* Rott. (Lepidoptera: Lycaenidae) during 1956. *Proc. R. Ent. Soc. Lond.* (A), **33,** 31-36.

Using a capture-recapture method an isolated colony showed a first brood numbers estimate of 2700 males and 700 females. Only a fortieth of these numbers were flying in September. *L. coridon*, present in the same area, showed a density of double that of *L. bellargus*.

Empson, D. W. (1958). Frit fly and the oat panicle. *Ann. Appl. Biol.* **46,** 479-482.

A brief assessment of grain damage related to the position of frit fly attack.

Gilbert, O. (1958). The life history patterns of *Nebria degenerata* Schaufuss and *N. brevicollis* (Fabricius) (Coleoptera, Carabidae). *J. Soc. Brit. Ent.,* **6,** 11-14.

Both species breed in autumn and overwinter as larvae. After emerging in the spring, they undergo a summer imaginal diapause during which the gonads mature.

Haggett, G. (1957). The habitat and habits of *Rhizedra lutosa* Hübn. (Lep., Noctuidae). *Entomologist,* **90,** 184-185.

Hill, A. R. (1957). The biology of *Anthocoris nemorum* (L.) in Scotland (Hemiptera: Anthocoridae). *Trans. R. Ent. Soc. Lond.* **109,** 379-394.

Gives details of the geographical and plant distribution, the life history and the generations, food and feeding habits, behaviour and copulation.

Hillman, E. M. [1958]. Devilsden Wood Survey: Birds. Some comparisons with other woodlands. *Lond. Nat.* **37** (1957), 186-189.

The densities of territories of 8 common birds during 1954-57 in three woods in Surrey and Kent that show some broadly similar vegetative characteristic, but differ in variety of plant, species, dampness, denseness and amount of human disturbance are compared and shown as histograms. In general, the relative populations were similar in all three. Increases in densities from year to year did not exceed 100 per cent or reach 50 per cent. Human disturbance apparently had no adverse effect and was probably offset by access to open areas and gardens. Willow-warblers were more than twice as common as chiffchaffs in the two oakwoods, but their numbers were equal in the mixed wood in the year for which records are available.

Hines, W. J. W. (1958). Larval responses to gravity and humidity in *Tenebrio molitor* L. (Coleoptera: Tenebrionidae). *Entolomolgist,* **91,** 112-114.

In laboratory experiments, the larvae showed negative geotaxis in dry and, to a less extent, in moist bran, but were sometimes unable to move upwards through moist bran, either because a relative humidity of 95 per cent was preferred to one of 50, or to avoid relative humidities exceeding 65 per cent.

Homes, R. C. [1958]. Changes in the bird life of the London area since 1900. *Lond. Nat.* **37** (1957), 22-35.

The major changes in the abundance and status of birds between 1900 and 1957 are reviewed systematically and the environmetal changes that have influenced them are summarized. Numbers of individuals and species of aquatic birds, both residents and winter visitors, and numbers of Corvidae and predatory birds formerly persecuted by game-keepers have increased, and heathland and ground-nesting birds have decreased. 31 vagrants or rare winter migrants recorded in the area for the first time between 1945 and 1956 are listed.

Hooper, J. H. D. (1958). Bat erosion as a factor in cave formation. *Nature, Lond.* **182,** 1464.

Argues, with some evidence from Buckfastleigh caves, that roof pockets in caves are natural formations and cannot be produced by erosion by roosting bats.

Hussey, N. W. & Parr, W. J. (1958). A genetic study of the colour forms found in populations of the greenhouse red spider mite, *Tetranychus urticae* Koch. *Ann. Appl. Biol.* **46,** 216-220.

There are two forms of *Tetranychus urticae* in Britain: one with green summer females and the other with reddish-brown females. The latter does not hibernate. The forms are subgenerically distinct, but hybrids of low fertility can occur. It is suggested that the reddish-brown form is distinct from *T. cinnabarinus* Bois.

Ibbotson, A. (1958). The behaviour of frit fly in Northumberland. *Ann. Appl. Biol.* **46,** 474-479.

Daily activity of frit fly, *Oscinella frit,* related to time, temperature and humidity.

Jepson, W. F. & Southwood, T. R. E. (1958). Population studies on *Oscinella frit* L. *Ann. Appl. Biol.* **46,** 465-474.

A phenological study of frit fly over a seven-year period at Silwood Park, Berkshire.

Lack, D. (1958). The return and departure of swifts *Apus apus* at Oxford. *Ibis,* **100,** 477-502.

A nightly check of roosting birds during six years' study showed that the return in spring varied by nine days, and was delayed only by a cold northerly airstream. Parents usually stayed for a few days after the young had gone, presumably to put on fat. This period was shorter in the case of late than of early broods, and was prolonged in years of bad weather in July. (See also 1956, *Ibis,* **98,** 606-619. Abstract in 1958, *J. Anim. Ecol.* **27,** 173.)

Lane, C. & Rothschild, M. (1957). Notes on the habitat of the Wood White (*Leptidia sinapis* L.) and Chequered Skipper (*Carterocephalus palaemon* Pallas). *Entomologist*, **90**, 271-272.

L. sinapis now frequents wide rides, instead of the heavily timbered areas, in a wood in Northamptonshire in which large areas have in recent years been felled or replanted. *C. palaemon*, which 30 years ago occurred in grassy rides, now frequents rough grass and scrub on the outskirts of the wood and has become considerably more numerous.

Laughlin, R. (1958). Desiccation of eggs of the crane fly (*Tipula oleracea* L.). *Nature, Lond.* **182**, 613.

Experimental analysis of effects of low humidities on eggs shows that after the first day natural conditions are rarely severe.

Leston, D. (1958). The habitat of *Hallodaphus rufescens* (Burm.) (Hem., Miridae) in southern England. *Ent. Mon. Mag.* **94**, 70.

Details of the habitat of the rare mirid bug *Hallodaphus rufescens* are given.

London Natural History Society [1958]. The survey of Bookham Common. Sixteenth Year. *Lond. Nat.* **37** (1957), 56-79.

A progress report includes notes on the increase in rabbits since 1954, feeding niches of woodland birds, and breeding by woodcock, records for four Agromyzids new to science collected on the Common, and a list of Crustacea from ponds, ditches and streams. Other papers include one recording the use of a bird's nest as a feeding site by a long-tailed field-mouse.

Mittler, T. E. (1958). The excretion of honey-dew by *Tuberolachnus salignus* (Gmelin) (Homoptera: Aphididae). *Proc. R. Ent. Soc. Lond.* (A), **33**, 49-55.

Discusses the results of quantitative measurements of this excretion by the aphid throughout its development. The rate of water lost from the general body surface is small compared to the honey-dew excretion. The effects of temperature, wind and ants are related to the excretory mechanism.

Nicholson, A. J. (1957). The self-adjustment of populations to change. *Cold Spring Harb. Symp. Quant. Biol.* **22**, 153-173.

Using data from laboratory populations of blowflies, demonstrates that species automatically, through density governed reactions, adjust to their circumstances and so are enabled to survive in spite of great changes of environment without developing new adaptations.

Nicholson, E. M. (1958). The modern naturalist. *Discovery*, **19**, 456-459.

The role of the amateur naturalist in current biology, with particular stress on ecological studies, as exemplified by the work of the London Natural History Society.

Norris, J. D. (1958). Observations on the control of mite infestations in stored wheat by *Cheyletus* spp. (Acarina: Cheyletidae). *Ann. Appl. Biol.* **46**, 411-422.

The domination of the grain mite *Acarus siro* L. by a predatory *Cheyletus* sp. in imported wheat in store. Dense populations of *A. siro* and *Glycyphagus destructor* Schr. were also eliminated by *C. eruditus* Schr.

Scott, H. (1958). Migrant millipedes and centipedes entering houses. *Ent. Mon. Mag.* **94**, 73-77.

A detailed description is given of the way in which the common black millipede *Tachypodoiulus niger* invaded a house over a period of years. A note is also given of the entry of a centipede.

Sevastopulo, D. G. (1958). Protective devices of endopterygote pupae. *J. Soc. Brit. Ent.* **6**, 2-4.

Some additions to the examples discussed by Hinton, H. E. (1955) *Trans. Soc. Brit. Ent.* **12**, 49-92.

Strickland, A. H. (1958). Frit-fly attack and yield of oats. *Ann. Appl. Biol.* **46**, 486-493.

The effects of frit-fly infestation on oat yields and on tiller production, assessed from randomized block experiments.

Thompson, J. L. Cloudsley- (**1958**). The effect of wind upon the nocturnal emergence of woodlice and other terrestrial arthropods—1. *Ent. Mon. Mag.* **94,** 106-108.

Observations are described which attempt to relate windspeed to the nocturnal activity of some arthropods and snails. It was found that the woodlice showed a fairly definite inverse relationship to windspeed.

Thompson, J. L. Cloudsley- & Sankey, J. H. P. (**1958**). Some aspects of the fauna of the district around Juniper Hall, Mickleham, Surrey. *Ent. Mon. Mag.* **94,** 43-47.

Brief notes are given on a series of observations on the terrestrial fauna of a limited area, including notes on micro-climate, protective coloration and general distribution.

Waterhouse, E. L. & Sanderson, A. R. (**1958**). Geographical colour polymorphism and chromosome constitution in sympatric species of sawflies. *Nature, Lond.* **182,** 477.

A brief note on breeding incompatibility, larval colour polymorphism and inter-breeding or not between species of *Tenthredo*.

Winslow, R. D. (**1958**). Eelworm control. Some aspects of past and present research. *Agriculture,* **65,** 66-69.

The predators of eelworms include Collembola, mites and nematodes of the genus *Monochus*; parasites include bacteria and fungi. Crop rotation is the best method of control.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Alam, S. Mashhood. (**1957**). The taxonomy of some British Encyrtid parasites (Hymenoptera) of scale insects (Coccidoidea). *Trans. R. Ent. Soc. Lond.* **109,** 421-466.

Provides a key to thirteen genera with specific keys where applicable.

Andrewartha, H. G. & Browning, T. O. (**1958**). Williamson's theory of interspecific competition. *Nature, Lond.* **181,** 1415.

Criticizes Williamson's theory of interspecific competition on the grounds of its abstraction from nature. Williamson replies.

Blackith, R. E. (**1958**). Nearest-neighbour distance measurements for the estimation of animal populations. *Ecology* **39,** 147-150.

Experimental comparisons of capture-recapture and nearest-neighbour estimates of grasshopper populations showed good agreement with Craig's formula for the latter, but not with Clark and Evans.

Collin, J. E. (**1958**). Notes on some British species of *Fannia* (Dipt., Muscidae), with the description of a new species. *Ent. Mon. Mag.* **94,** 86-92.

Details of a number of species of the genus *Fannia* are given which will facilitate identification, together with the description of a new species.

Collingwood, C. A. (**1958**). The ants of the genus *Myrmica* in Britain. *Proc. R. Ent. Soc. Lond.* (A), **33,** 65-75.

Provides keys to the males, queens and workers of the seven British species of this genus. Their distribution, habits and main variations are briefly discussed.

Collingwood, C. A. (**1958**). A key to the species of ants (Hymenoptera: Formicidae) found in Britain. *Trans. Soc. Brit. Ent.* **13** (5), 69-96.

Cottam, G., Curtis, J. T. & Catana, A. J. (**1957**). Some sampling characteristics of a series of aggregated populations. *Ecology,* **38,** 610-622.

Discusses homogeneity and complexity of aggregation patterns in natural populations and proposes three indices of aggregation using distance methods.

Emsley, M. G. (**1958**). A technique for the examination of the feeding mechanism in phytophagous Heteroptera. *Proc. R. Ent. Soc. Lond.* (A), **33,** 93-94.

A method of electrocuting Heteroptera in the act of feeding is described.

Fager, E. W. (1957). Determination and analysis of recurrent groups. *Ecology*, **38,** 586-595.

Uses ranking correlations for analysis of catch samples of several species and discusses a new index of affinity based on presence and absence.

Hynes, H. B. N. (1957). The British Taeniopterygidae (Plecoptera). *Trans. R. Ent. Soc. Lond.* **109,** 233-243.

Provides a key to the nymphs and adults of the British species.

Jackson, D. J. (1958). A further note on a *Chrysocharis* (Hym., Eulophidae) parasitizing the eggs of *Dytiscus marginalis L.*, and a comparison of its larva with that of *Caraphractus cinctus* Walker (Hym., Mymaridae). *J. Soc. Brit. Ent.*, **6,** 15-22.

Descriptions and figures of larvae of *Chrysocharis* sp. and of *C. cinctus* which are easily distinguishable, that of *Chrysocharis* sp. being much larger, segmented and with well developed mandibles.

Laurence, B. R. (1957). The British species of *Trichocera* (Diptera: Trichoceridae). *Proc. R. Ent. Soc. Lond.* (A), **32,** 132-138.

Provides a key for the separation of the British species.

Macan, T. T. (1958). A comparison of the nymphs of the British species of the genus *Ephemera*. *J. Soc. Brit. Ent.*, **6,** 27-33.

Miles, P. W. (1958). The stylet movements of a plant-sucking bug, *Oncopeltus fasciatus* Dall. (Heteroptera: Lygaeidae). *Proc. R. Ent. Soc. Lond.* (A), **33,** 15-20.

Describes a method for observing stylet activity by cinephotography.

Morison, G. D. (1957). A review of British glasshouse Thysanoptera. *Trans. R. Ent. Soc. Lond.* **109,** 467-520.

Includes a key to the adults with notes on habits, life history, bionomics, tolerance to temperature and humidity, transmission of virus diseases, predators and parasites and control for nearly forty British species belonging to the Thripidae and Phlaeothripidae.

Nicholson, A. J. (1955). Density governed reaction, the counterpart of selection in evolution. *Cold Spring Harb. Symp. Quant. Biol.* **20,** 288-293.

Discusses the operation of density governed reactions on the establishment of new mutants which are more fit than the original population, and shows how selection may progress because of this in the absence of environmental change.

Nicholson, A. J. (1958). Dynamics of insect populations. *Ann. Rev. Ent.* **3,** 107-136.

A critical review of theories of population dynamics and a reassertion of the well-known theory of population regulation by density governed reactions.

Richards, T. J. (1958). Observations on the nymphs of seven Tettigononioids (Orthopt., Tettigoniidae, Meconematidae, Conocephalidae, Phaneropteridae). *Entomologist*, **91,** 53-66.

Observations, mostly under cage conditions, in South Devon on hatching, moulting, growth, habits and food. A key to the first-instar nymphs and a table showing the morphological changes following each moult in five species are included.

Sands, W. A. (1957). The immature stages of some British Anthocoridae (Hemiptera). *Trans. R. Ent. Soc. Lond.* **109,** 295-310.

Includes keys to the eggs and nymphs of twelve species.

Skellam, J. G. (1958). The mathematical foundations underlying the use of line transects in animal ecology. *Biometrics*, **14,** 385-400.

Theoretical and empirical analysis of the use of line transects in studies of population densities, with special reference to the variance of the estimates.

Slobodkin, L. B. (1958). Meta-models in theoretical ecology. *Ecology*, **39,** 550-551.

Discusses three models of classification of population phenomena, in terms of foodwebs, age-specific fertility and mortality rates and recruitment rates in relation to equilibria and oscillations.

Solomon, M. E. & Varley, G. C. (1958). Meaning of density-dependence and related terms in population dynamics. *Nature, Lond.* **181,** 1778-1781.

Directs attention to confusions in the use of the term 'density-dependent'. Solomon advocates the use of three new terms, Varley being opposed to this.

Spencer, K. A. (1957). Notes on the British species of *Melanagromyza* Hendel (Diptera: Agromyzidae), with the description of four new species, and also of three new species from Germany. *Proc. R. Ent. Soc. Lond.* (B), **26,** 179-188.

Includes a key to the British species of this genus.

Stokoe, R. (1958). The spring plumage of the cormorant. *Brit. Birds,* **51,** 165-179.

White heads and green gloss are not valid field characters for distinguishing the continental race *Phalacrocorax carbo sinensis* from the British *Ph. c. carbo.* Most British cormorants have a greenish gloss, and about 15% of adults have white heads for a short time before incubation begins, the degree of whiteness increasing with age. Over 1500 birds were examined.

Thompson, J. L. Cloudsley- (1957). Some comments on the natural control of animal populations with especial reference to insects. *Entomologist,* **90,** 195-203.

It is concluded from this discussion of the existing theories and opinions regarding the natural regulations of animal populations that restrictions by territory, suitable nesting sites, and shelters are probably the most important density-dependent factors controlling larger animals, whereas insect populations are probably more frequently checked by natural enemies and the importance of food shortage in regulating them has in most cases been exaggerated.

3. PARASITES

Freeman, R. F. H. & Llewellyn, J. (1958). An adult digenetic trematode from an invertebrate host: *Proctoeces subtenuis* (Linton) from the lamellibranch *Scrobicularia plana* (Da Costa). *J. Mar. Biol. Ass. U.K.* **37,** 435-457.

Includes a review of the species of *Proctoeces.*

Harding, J. P. & Wheeler, A. C. (1958). Heavy infestation by the parasitic copepod *Lernaeenicus* of sprats in the River Crouch. *Nature, Lond.* **182,** 542-543.

More than 30% infestation of sprats with *Lernaeenicus sprattae* and *L. eucrasicola*; with notes on relative occurrence and on the characters distinguishing the parasites and a brief statistical analysis of the size distribution of the hosts.

Hincks, W. D. (1958). *Myrmecobosca mandibularis* Maneval (Hym., Braconidae), a myrmecophilous aphid parasite in Britain. *Ent. Mon. Mag.* **94,** 20-21.

A short description is given of the braconid *Myrmecobosca mandibularis,* together with notes on its habits.

Jackson, D. J. (1958). Notes on some nematodes and trematodes infesting water beetles. *Ent. Mon. Mag.* **94,** 109-111.

The presence of nematodes under the elytra of several species of water beetles is noted, and the presence of nematode and trematode eggs in the body cavity of water beetles is recorded.

Jennings, A. R. & Soulsby, E. J. L. (1958). Disease in a colony of black-headed gulls *Larus ridibundus. Ibis,* **100,** 305-312.

A colony of more than 600 pairs on Alderfen Broad, Norfolk, suffered heavy mortality in 1956. Many chicks died from chilling, and 27% of a sample of 33 dead chicks died from heavy parasitic infection by trematodes, *Diplostomum spathaceum* and, to a less extent, *Cryptocotyle lingua.* Mortality was highest in the most crowded part of the colony.

Kabata, Z. (1957). *Lernaeocera obtusa* n.sp., a hitherto undescribed parasite of the haddock (*Gadus aeglefinus* L.). *J. Mar. Biol. Ass. U.K.* **36,** 569-592.

Contrasts distribution of the new species, on fishes in offshore waters, with that of *L. branchialis* on cod and whiting mainly in inshore localities.

Leatherdale, D. (1958). A host catalogue of British entomogenous fungi. *Ent. Mon. Mag.* **94,** 103-105.

A list is given of fungi attacking insects and some arachnids, arranged entomologically and covering eight insect orders.

Leston, D. (1958). Further notes on parasitism of *Miridae* (Hem.) by Braconidae (Hym.) in Britain. *Ent. Mon. Mag.* **94,** 35.

Records are given for braconid parasites on four species of capsid bugs.

Llewellyn, J. (1957). The larvae of some monogenetic trematode parasites of Plymouth fishes. *J. Mar. Biol. Ass. U.K.* **36,** 243-259.

Describes and classifies eleven new oncomiracidia.

Pearce, E. J. (1958). *Tychus niger* (Payk) (Col., Pselaphidae) infected with Uropodid mites. *Ent. Mon. Mag.* **94,** 17.

The beetle *Tychus niger* is described as transporting nymphal mites.

Rothschild, M. (1957). The sand martin flea at Oundle, Northamptonshire. *Entomologist,* **90,** 216.

Fleas taken from a sand-martin's nest at Oundle comprised *Ceratophyllus styx jordani* (the northern sub-species) and several *C. gallinae*. Since sand martins here and elsewhere in the country now nest in masonry, where they are likely to pick up the latter flea from sparrows and starlings, they may become regular hosts for it.

Rothschild, M. (1957). Breeding the rabbit flea (*Spilopsylla cuniculi* (Dale)) in captivity. *Entomologist,* **90,** 304-305.

Successful breeding and establishment was possible only on rabbits kept under semi-wild conditions, when infestation was at least as heavy on domestic as on wild ones. This flea appears to be very sensitive to environmental changes, to which it responds by rapid dispersal.

Rothschild, M. (1958). Fleas from the nest of the St. Kilda wren (*Troglodytes troglodytes hirtensis* (Seeb.). *Entomologist,* **91,** 76.

Lists of fleas from nests collected after the young had flown and from deserted nests. Seven species are represented, including four not hitherto known from St. Kilda.

Salt, G. (1958). Parasite behaviour and the control of insect pests. *Endeavour,* **17,** 145-148.

A behaviour study of *Trichogramma* (Hymenoptera) parasitizing eggs of the grain moth, *Sitotroga*.

Smith, K. M. & Williams, R. C. (1958). Insect viruses and their structure. *Endeavour,* **17,** 12-21.

This introduction to insect viruses gives a brief description of their classification into polyhedroses, granuloses and non-encapsulated forms. Some attention is given to the factors responsible for the spread of virus diseases, of which the most important is ingestion. Two viruses are considered in more detail, and illustrated with some remarkable plates: TIV (*Tipula* iridescent virus) and a polyhedral virus, both infecting larvae of the cranefly *Tipula paludosa*.

Styles, J. H. (1958). Host records of two British Ichneumonidae (Hym.). *Ent. Mon. Mag.* **94,** 111.

The ichneumon flies *Hypsantyx lituratorius* and *Aoplus lariciatae* are recorded from the pine sawfly, *Diprion pini*, and the moth *Eupithecia lariciata* respectively.

Thompson, G. B. (1958). The parasites of British birds and mammals XXXIII. The insect ectoparasites of the house-sparrow (*Passer d. domesticus* L.) *Ent. Mon. Mag.* **94,** 1-5.

Collected records of insect ectoparasites on the house sparrow are given, with remarks on the possibilities of parasite transmission by sparrows.

4. FOOD AND FOOD HABITS

Allen, A. A. (1958). Prey of *Athcta* (*Acrotona*) *fungi* Grav. (Col., Staphylinidae). *Ent. Mon. Mag.* **94,** 54.
The rove beetle *Atheta fungi* is recorded as feeding on Collembola.

Allen, A. A. (1958). Polyphagy in *Batodes angustoriana* Haw. (Lep., Tortricidae). *Ent. Mon. Mag.* **94,** 62.
The larvae of the moth *Batodes angustoriana* are recorded as having been reared on a variety of food plants, and it is considered that the species must be regarded as polyphagous.

Allen, A. A. (1958). Notes on the larval feeding-habits, etc., of *Lebia* spp. (Col., Carabidae) especially *chlorocephala* Hoff. *Ent. Mon. Mag.* **94,** 95.
It is pointed out that although the carabid beetle *Lebia chlorocephala* is normally a predator on the leaf beetle *Chrysomela varians*, the relative scarcity of this latter beetle in Britain makes it likely that the carabid is not restricted to *C. varians*.

Baker, C. S. Wood- (1958). The oviparous female of *Vesiculaphis theobaldi* Tak. and notes on its food-plants (Hem., Aphididae). *Ent. Mon. Mag.* **94,** 100-102.
The oviparous female of the aphid *Vesiculaphis theobaldi* is described and an account of the egglaying given. The food plants are also described.

Barden, E. D. (1958). Two Diptera reared from elder stems in Scotland. *Ent. Mon. Mag.* **94,** 42.
Larvae of the flies *Pegohylemyia fugax* and *Helomyza ustula* are recorded in the pith of elder stems.

Broadhead, E. (1958). Some records of animals preying on psocids. *Ent. Mon. Mag.* **94,** 68-69.
Records of predators on psocids are given including spiders, mites and insects.

Crowley, T. E. (1958). *Viviparus* eaten by crows. *J. Conch.* **24,** 280.
An account of carrion crows preying upon the river snail, *Viviparus viviparus*.

Dales, R. P. (1957). Some quantitative aspects of feeding in sabellid and serpulid fan worms. *J. Mar. Biol. Ass. U.K.* **36,** 309-316.
Estimates of filtering rates of several species and comparisons with *Chaetopterus* and other invertebrates.

Grensted, L. W. (1958). Ants visiting the passion flower *Passiflora caerulea* L. *Ent. Mon. Mag.* **94,** 33.
The black ant *Lasius niger* is recorded as feeding on the petals of the passion flower.

Groves, E. W. [1958]. A bird's nest feeding site of the long-tailed field-mouse. *Lond. Nat.* **37** (1957), 65-66.
An old bullfinch's nest situated in a rose-bush and filled with the skins of hips and the empty husks of hip seeds bearing teeth marks had evidently been used as a feeding site by a mouse, probably *Apodemus sylvaticus*. A pile of similar hip remains was on the ground beneath the bush.

Lane, C. (1957). Swallows and house martins taking moths near an m.v. trap. *Entomologist,* **90,** 297.
Moths taken, while being removed from the trap, by these birds on the wing included the swallow-tailed moth (*Ourapteryx sambucaria*) and the yellow underwing (*Triphaena pronuba*).

Laurence, B. R. (1958). A Strepsipteron as the prey of an Empid fly. *Ent. Rec.* **70,** 197.
A female of *Bicellaria sulcata* was captured with a male *Elenchus* as prey.

Lewis, E. (1958). Two predators of *Rhagonycha fulva* (Scop.) (Col., Cantharidae). *Ent. Mon. Mag.* **94,** 31.
Two beetle predators are recorded as preying on the soldier beetle *Rhagonycha fulva*.

Mason, E. C. (1958). Notes on the life-history and host range of the tortrix *Cnephasia longana* (Haworth) (Lep., Tortricidae). *Ent. Mon. Mag.* **94,** 79-80.
Caterpillars of the moth *Cnephasia longana* were collected and reared, and notes on the life history are given. A large range of host plants is given.

Parmenter, L. (1958). *Tettigonia viridissima* L. (Orth., Tettigoniidae) as prey of the song thrush. *Ent. Mon. Mag.* **94,** 119.
The common song thrush is reported as feeding on the great green grasshopper.

Pontin, A. J. (1958). A preliminary note on the eating of aphids by ants of the genus *Lasius* (Hym., Formicidae). *Ent. Mon. Mag.* **94,** 9-11.
Details are given of observations on the eating of aphids by ants, and it is suggested that the protein/carbohydrate ratio of the ant food is important.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Andrews, C. H. (1958). An arctic *Spilogona* new to Britain, on Ben Lawers (Diptera: Muscidae) *J. Soc. Brit. Ent.* **6,** 26.
Records *S. alpica* Zett. in Perthshire.

Ashe, G. H. (1958). Dimorphism in *Arena octavii* (Fauv.) (Col., Staphylinidae). *Ent. Mon. Mag.* **94,** 96.
Brachypterous forms of the rove beetle *Arena octavii* are noted.

Barbier, P. G. R. (1958). An annotated list of birds observed in East Montgomeryshire. *Nature in Wales,* **4,** 624-628.
An annotated list of 120 species seen from August 1954 to August 1958, including Rough-legged Buzzard, Marsh Harrier, Hen Harrier and Osprey.

Baynes, E. S. A. (1957). The Lepidoptera of Tory Island, Co. Donegal. *Entomologist,* **90,** 310-313.
A list of species taken in 1951-56 at the lighthouse on this isolated island situated about 9 miles from the extreme North-west of County Donegal.

Bradley, J. D. (1958). Microlepidoptera from the Islands of Canna and Sanday, Inner Hebrides. *Entomologist,* **91,** 9-14.
A list, with numbers and habitats, of species collected during July 1956 that is stated to include some not previously recorded from the Hebrides.

Bradley, J. D. & Fletcher, D. S. 1958. Lepidoptera records from the Isle of Rhum (Inner Hebrides). *Entomologist,* **91,** 126-131.
A list, based on collections in July 1956 and 1957, with localities and numbers, including several species not hitherto recorded from the island.

Brindle, A. 1958. New Diptera records for Lancashire, Yorkshire and Westmoreland. *Ent. Rec.* **70,** 211-213.
New county records, mostly for Yorkshire, for six Tipulids and six species of six other families.

Brinkhurst, R. O. 1957. Records of freshwater invertebrates from the Spey Valley near Kingussie, Inverness-shire. *Entomologist,* **90,** 260-268.
Lists of insects, mostly Ephemeroptera, Plecoptera and Trichoptera, for which numbers, dates and localities are given, and a few other invertebrates that were collected from stones and in detritus and aquatic vegetation in streams, lakes and ponds during July-August 1954 and early April 1956, with descriptions of the habitats and, for the streams, a discussion of the results with reference to the findings of other workers.

Clark, D. J. (1958). *Gymnosoma* (*Stylogymnomyia*) *nitens* Meig. (Diptera: Tachinidae) new to Britain. *Entomologist,* **91,** 100.

Corbin, P. G. (1958). A new British fish (*Gobius forsteri*). *Nature, Lond.* **181,** 1659.
Describes a new goby taken during aqualung diving by G. R. Forster off the Devon and Cornwall coasts and off the European coast, with brief notes on habits and ecology.

Cowdy, S. (1958). Deer in the Chilterns. *Middle-Thames Nat.* **10,** 12-13.
Three species occur on the wooded escarpment near Wendover, roe, fallow and muntjac, all believed to be descendants from escapes from parks and zoos in the neighbourhood.

Crisp, D. T. & Heal, O. W. (1958). The Corixidae (O. Hemiptera), Gyrinidae (O. Coleoptera) and Cladocera (Subphylum Crustacea) of a bog in western Ireland. *Irish Nat. J.* **12,** 297-304, 318-24.
A survey of the distribution of three groups of invertebrates in the water bodies (classified into open lakes, closed lakes and lily-pools) of a bog near Cliffden, West Galway, in July 1955 and July 1956.

Davis, R. A. & Evans, L. Lloyd- (1958). Occurrence of the ship rat (*Rattus rattus* L.) in Hertfordshire. *Trans. Herts Nat. Hist. Soc.* **25,** 4-6.
This alien species is present in several premises along the River Lea, where it has been brought by barge.

de Worms, C. G. M. [1958]. The moths of London and its surroundings. *Lond. Nat.* **37** (1957), 136-178.
This final part contains notes on the localities, abundance, food plants and seasonal occurrence of the remaining species of Geometridae and the Hepialidae. (cf. 1957, *Lond. Nat.* **36,** 59-99, abstr. 1958, *J. Anim. Ecol.* **27,** 184.)

Duddington, J. H. (1958). Duneland Lepidoptera found inland in Lincolnshire. *Entomologist,* **91,** 49.
Eight essentially coastal species occur in an inland area of Lindsey. This Riding was formerly an island subject to sandstorms, from its tidal estuaries, that were particularly severe in the eleventh century and continued until the seventeenth.

Eltringham, S. K. & Hockley, A. R. (1958). Coexistence of three species of the wood boring isopod *Limnoria* in Southampton Water. *Nature, Lond.* **181,** 1659-1660.
The American *Limnoria tripunctata* exists with *L. lignorum* and *L. quadripunctata.* No evidence of interbreeding seen either in nature or in laboratory colonies.

Fonseca, E. C. M. d'Assis- (1958). *Fannia vespertilionis* Ringd. (Dipt., Muscidae) from bat roosts. *Ent. Rec.* **70,** 106-107.
This fly, hitherto known in Britain only from Herefordshire and Brecknockshire, was found in May 1957 in bat droppings from trees at two places in Gloucestershire. Larvae from droppings of *Nyctalus noctula* collected on 19 May gave rise to adults between June 24 and 3 July. The adults probably spend their entire life within the bat roosts.

Gair, R. & Taylor, C. E. (1957). Further records of Aphids of East Midlands counties. *Entomologist,* **90,** 204-210.
Localities, dates, food plants and attendant ant species for Aphids collected in Northamptonshire, and additional records for species from Derbyshire, Leicestershire, Nottinghamshire and Lincolnshire. (cf. 1954, *Northw. Nat* (N.S.) **2,** 512-525, abstr. 1956, *J. Anim. Ecol.* **25,** 205.)

Gardiner, B. O. C. (1958). Cambridgeshire's changing Lepidoptera. *Nature in Cambs.* **1,** 21-24.
A summary of changes during the past century; some 60 species have become extinct in the county, and several butterflies have not been recorded for over 20 years.

Gooding, R. U. (1957). On some copepoda from Plymouth, mainly associated with invertebrates, including three new species. *J. Mar. Biol. Ass. U.K.* **36,** 195-221.
Micropontius, Lichomolgus and *Conchyliurus* new to Plymouth.

Hannay, P. W. (1958). Corixids of Berkshire. *J. Soc. Brit. Ent.*, **6,** 5-6.
Tabulates species from 88 habitats with notes on distribution.

Harrison, J. W. Heslop- (1958). *Argynnis aglaia* L. in Co. Durham. *Entomologist,* **91,** 32.
A. aglaia was diminishing in eastern county Durham some 60 years ago, but has again become abundant during the past ten years, evidently following immigration from the south, since the southern form has replaced the northern.

Harrison, J. W. Heslop- (1958). Two Hemiptera-Heteroptera apparently new to Co. Durham. *Entomologist,* **91,** 45.
Acanthosoma interstinctum on birch and *A. dentatum.*

Harrison, J. W. Heslop- (1958). Lepidoptera in the Scottish Western Isles in 1957. *Entomologist,* **91,** 79-85.
Records from Harris, Ensay, Lewis and Rhum.

Harrison, J. W. Heslop- (1958). Two 'Micros' new to the Outer Hebrides. *Entomologist,* **91,** 49.
Argyroploce dimidiana on *Myrica gale* and *Lithocolletis stettinensis* from alder on Lewis. *L. stettinensis* is also recorded for the first time on Rhum.

Hinton, H. E. (1958). On the pupa of *Spalgis lemolea* Druce. *J. Soc. Brit. Ent.*, **6,** 23-25.
At a distance it may resemble bird excrement and nearby an anthropoid face.

Huggins, H. C. & Mere, R. M. (1958). *Crocidosema plebeiana* Zeller resident in the British Isles. *Entomologist,* **91,** 20-22.
Adults came to light at two places on Tresco in July 1957 and were collected near tree mallow (*Lavatera arborea*) at a third in September. Larvae were found in the seed-pods of the tree mallow.

Jackson, P. A. (1958). Movement of salmon on the River Erne. *Nature, Lond.* **182,** 543.
Records from the nylon-screen type counter at the fishpass over four fishing seasons show that fish are moving most between noon and dusk, and hardly at all during darkness.

Kettlewell, H. B. D. (1958). The larva of *Heliothis maritima septentrionalis* Hoffmeyer in Britain (Lep., Noctuidae). *Entomologist,* **91,** 27-29.
This larva, not hitherto known in Britain, was common on *Erica tetralix* by a bog in the New Forest in August-September 1957.

Kimmins, D. E. (1957). Notes on some British species of the genus *Hydropsyche* (Trichoptera). *Ent. Gaz.* **8,** 199-210.

Kingsbury, P. A. (1958). Deer at Ashridge. *Trans. Herts. Nat. Hist. Soc.* **25,** 2-3.
Two species fallow, and probably muntjac, both escaped from parks or zoos, present in this wooded park in the Chilterns.

Lack, D. (1958). Migrational drift of birds plotted by radar. *Nature, Lond.* **182,** 221-223.
Correlation of radar tracking of passerines from the East coast, mostly over the North Sea but some overland, with meteorological wind records at appropriate heights confirms that migrational drift occurs, particularly during overcast weather.

Leston, D. (1958). The distribution of waterbugs (Hemiptera-Heteroptera: Hydrocorisae) in Ireland. *Ent. Mon. Mag.* **94,** 26-31.
The distribution of twelve species of water bugs in Ireland is presented with the aid of maps.

Lewis, E. (1958). A flight swarm of *Helophorus affinis* (Marsh) (Col., Hydrophilidae). *Ent. Mon. Mag.* **94,** 42.
Numbers of the hydrophilid beetle *Helophorus affinis* are reported flying near the sea coast.

Longfield, C. (1957). Notes on the British Odonata (dragonflies) for 1954 and 1955. *Entomologist,* **90,** 44-49.

Macan, T. T. (**1957**). Some records of water-bugs in Scotland. *Ent. Gaz.* **8,** 236-241.

Magee, J. D. (**1958**). Notes on the bird life of Cassiobury Park, the West Herts. golf course and Whippendell Woods, Watford, 1909-1956. *Trans. Herts. Nat. Hist. Soc.* **25,** 16-26.

Contains many interesting examples of the effect of opening an area of woodland and parkland near a large town to public access.

Mann, K. H. (**1958**). Occurrence of an exotic oligochaete *Branchiura sowerbyi* Beddard, 1892, in the River Thames. *Nature, Lond.* **182,** 732.

Records the species in the Thames, with notes on a colony in the Bradford River Avon.

Miles, P. M. (**1958**). The Diamond Back Moth (*Plutella maculipennis* (Curt.)). *Nature in Wales,* **4,** 628-629.

A brief account of damage done in Wales by the Diamond Back Moth invasion from the Continent in the summer of 1958.

Naylor, E. (**1957**). The occurrence of *Idotea metallica* Bosc in British waters. *J. Mar. Biol. Ass. U.K.* **36,** 599-602.

A description of the species and its distribution.

Niblett, M. [**1958**]. The gall wasps of the London area. *Lond. Nat.* **37** (1957), 126-135.

Annotated lists of 53 Cynipid species and forms that attack oak and 22 that attack other plants, with food plants, part attacked, months in which galls are present, years and months in which the adults emerge, and localities, mostly in Surrey, but including some for Kent, Essex, Hertfordshire and Middlesex.

Payne, R. M. [**1958**]. The distribution of grasshoppers and allied insects in the London area. *Lond. Nat.* **37,** (1957), 102-115.

Information on the distribution of 25 Orthopteroids that have been recorded within a radius of 20 miles of St. Paul's Cathedral, with past and present localities, and notes on their seasonal occurrence, habitats and stridulation.

Price, L. (**1958**). Some notes on the Microlepidoptera of Gloucestershire. *Ent. Rec.* **70,** 152-153.

Includes a few new county records as well as recent confirmations of old ones.

Russell, F. S. (**1958**). A new species of *Atolla. Nature, Lond.* **181,** 1811-1812.

Adds *Atolla parva* n.sp. to *A. wyvillei* and *A. vanhöffeni* in the north Atlantic, with a brief description.

Russell, H. M. (**1958**). Yorkshire Agromyzidae (Diptera) Part 1. *J. Soc. Brit. Ent.,* **6,** 7-10.

A preliminary list of 30 species taken in Yorkshire, either as leaf miners or as adults.

Ryland, J. S. (**1958**). *Bugula simplex* Hincks, a newly recognized polyzoan from British waters. *Nature, Lond.* **181,** 1146-1147.

A partial description of the species and its distribution.

Scott, H. (**1958**). *Humerobates rostrolamellatus* Grandjean, an oribatid mite, invading a house. *Ent. Mon. Mag.* **94,** 69-70.

The mite *Humerobates rostrolamellatus* is recorded as entering a house in numbers, and it is suggested that the treatment of the exterior of the house with a wood preservative may have been responsible for the invasion.

Shearer, W. M. (**1958**). The movements of salmon tagged in the sea, Montrose, 1954, 1955. *Scottish Home Dept., Freshw. Salm. Fish. Res.* **20,** 1-11.

Describes methods and results with *Salmo salar* in Scotland.

Southward, A. J. (**1958**). Abundance of Pogonophora. *Nature, Lond.* **182,** 272.

Records Pogonophora from six stations off the continental slope between 300 and 700 fathoms, and also from Dingle Bay, W. Ireland, in only 80 to 90 fathoms.

Southward, A. J. & Southward, E. C. (1958). Pogonophora from the Atlantic. *Nature, Lond.* **181,** 1607.

A first record from the continental slope southwest of Britain, at 700 f. on a muddy bottom.

Southwood, T. R. E. (1957). Notes on some Mirids (Hem.) collected on Bookham Common. *Entomologist,* **90,** 301-303.

The three species dealt with include *Capsodes gothicus,* which was taken in numbers on *Lotus uliginosus.* The food plant was hitherto unknown.

Stelfox, A. W. (1958). A short history of the known occurrences of *Helicella gigaxi* (L. Pfeiffer) in Ireland. *J. Conch.* **24,** 283-284.

The known localities and habitats of a land snail very rare in Ireland.

Stroyan, H. G. L. (1957). Further additions to the British aphid fauna. *Trans. R. Ent. Soc. Lond.* **109,** 311-360.

Records 41 additions to the British fauna.

Stuart, T. A. (1957). The migrations and homing behaviour of brown trout (*Salmo trutta* L.). *Scottish Home Dept., Freshw. Salm. Fish. Res.* **18,** 2-26.

Describes investigations in Scottish lochs on young and mature fish.

Veysey, C. M. (1958). Ham Island sewage farm: some further notes on the bird life. *Middle-Thames Nat.* **10,** 3-7.

Notes on the birds of this artificial marsh habitat for 1952-56.

Wheeler, A. C. [1958]. The fishes of the London area. *Lond. Nat.* **37** (1957), 80-101.

Information on the distribution and abundance of 40 species and hybrids that occur or have occurred in the London area, with localities for the commoner ones, and a discussion of the factors in the urban and industrial development that have affected their ecology. Industrial pollution and, to a less extent, the construction of weirs and locks, embanking and dredging, and the culverting of the lesser rivers have led to the disappearance or reduction of some species, whereas the construction of reservoirs and canals and the introduction of endemic and alien species have led to the establishment of others.

Williamson, K. (1958). Autumn immigration of redwings *Turdus musicus* into Fair Isle. *Ibis,* **100,** 582-604.

Outlines the normal pattern of immigration and compares the meteorological conditions governing the migrations of *Turdus m. musicus* and *T. m. coburni.* An unusually large invasion of *coburni* in 1956 is attributed to special weather factors rather than a population peak. Identification of the races was based on laboratory examination of trapped birds.

Woodroffe, G. E. (1957). *Phytocoris insignis* Reuter (Hem.)—a Mirid hitherto unrecognized in Britain. *Entomologist,* **90,** 258-259.

This Mirid, hitherto misidentified as a small, dark form of *P. varipes,* occurs on *Calluna* on heathlands in Britain. Characters separating it from *P. varipes* are included.

Woodroffe, G. E. (1958). Biological notes on some Hemiptera-Homoptera from Devon and Cornwall. *Ent. Mon. Mag.* **94,** 24.

Collections of various Hemiptera-Homoptera from coastal areas are described with particular reference to the food plant.

Woodroffe, G. E. (1958). A note on *Pilophorus confusus* (Kb.), *Globiceps cruciatus* Reut. and *Adelphocoris ticinensis* (Mey-Duer) (Hem., Miridae) at Virginia Water and *Acompus rufipes* Wolff (Hem., Lygaeidae) at Chobham, Surrey. *Ent. Mon. Mag.* **94,** 64.

The occurrence of three mirid bugs in a sand pit is recorded and differences between the nymphal and adult habitat described. Notes are also given on the Lygaeid bug *Acompus rufipes.*

Yeo, P. F. (1958). Some spring bees found in Cambridge gardens. *Nature in Cambs.* **1,** 32-33.

Notes on solitary bees likely to be found in gardens and how to identify them.

6. STUDIES ON BEHAVIOUR

Dixon, A. F. G. (1958). The protective function of the siphunculi of the nettle aphid, *Microlophium evansi* (Theob.) (Hem., Aphididae). *Ent. Mon. Mag.* **94,** 8.

Observations of attacks on aphids by coccinellid larvae showed that under certain conditions, the aphid may escape from the coccinellid larvae by directing an oily substance from the siphunculi on to the mouthparts of the attacking larvae.

Free, J. B. (1957). The effect of social facilitation on the ovarial development of bumble-bee workers. *Proc. R. Ent. Soc. Lond.* (A), **32,** 182-184.

The number of bees present influences ovarial development in workers when temperature is not a limiting factor. However, workers kept in isolation sometimes developed sufficient eggs to be laid. Differences are possibly explained by the amount of food consumed by workers belonging to groups of different sizes.

Long, D. B. (1958). Host plant location by larvae of the Wheat Bulb Fly (*Leptohylemyia coarctata* Fallén). *Proc. R. Ent. Soc. Lond.* (A), **33,** 1-8.

Results, from the inoculation of prepared plants and by direct observation of movement in dishes, show that larvae move upwards at a fairly steep angle from the egg site and then horizontally into the surface layers of the soil. This involves a larval response to attractant materials exuded from the stem and root zones of the young wheat plants.

Minton, C. D. T. (1958). Magpie's rapid replacement of dead mate. *Brit. Birds,* **51,** 309.

A shot mate was replaced in two days and in seven hours respectively in successive years.

Payne, R. M. (1958). The stridulation of *Chorthippus vagans* (Eversm.) (Orth., Acrididae) and *Platycleis denticulata* (Panz.) (Orth., Tettigoniidae). *Ent. Mon. Mag.* **94,** 80.

The chirping rate of two grasshoppers is described.

Richards, O. W. (1958). *Formica rufa* L. (Hym., Formicidae) nesting in a tree. *Ent. Mon. Mag.* **94,** xv.

A nest of the ant *Formica rufa* in a hollow birch is recorded.

Rollin, N. (1958). Late season singing of the yellowhammer. *Brit. Birds,* **51,** 290-303.

Observations in Northumberland (*c.* 55° N.) and Norway (63-69° N.) showed that in Britain yellowhammers sing much in August: one bird sang 3482 songs in one day, occupying more than 12 hours in the singing phase. In Arctic Norway they sing less late in the season, and cease in July. Continuous light, lack of night sleep, and less song competition are factors that may reduce song in high latitudes.

Roberts, E. L. (1958). Unusual nest of song thrush. *Brit. Birds,* **51,** 275.

The nest lacked the usual lining.

Simpson, J. (1957). Observations on colonies of honey-bees subjected to treatments designed to induce swarming. *Proc. R. Ent. Soc. Lond.* (A), **32,** 185-192.

Attempts were made to induce colonies to swarm by crowding the bees in the hive, by depriving them of larval brood, giving them extra larval or pupal broods and by a combination of the first two treatments.

Crowding plus removal of eggs was invariably followed by swarming. Brood food surplus is not essential, and when acting alone is insufficient for the commencement of swarm preparations.

Thomson, A. L. (1958). Social flying of ravens. *Brit. Birds,* **51,** 246-247.

Further references concerning the pair composition of social gatherings of ravens. (See Hewson, R. 1957, *Brit. Birds,* **50,** 432-434. Abstract in 1958, *J. Anim. Ecol.* **27,** 189.)

Thorpe, W. H. (1958). The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis,* **100,** 535-570.

Research at Madingley Field Ornithological Station showed that songs of chaffinches are an integration of inborn and learned patterns. Birds hand-reared in isolation had simpler songs than wild ones. Chaffinches rarely copy sounds not of chaffinch origin, and such sounds are kept for non-communicative subsong. They can normally learn song patterns only during the first 13 months of life, the peak period of learning being a few weeks towards the end of this time.

7. REPORTS OF ORGANIZATIONS

Freshwater Biological Association (1958). 26th Annual Report for 1957-58. (The Ferry House, Far Sawrey, Ambleside, Westmorland, 4s.)

Summarizes a wide range of research of interest to ecologists, under the headings of hydrology, chemistry, bottom deposits, algology, mycology, bacteriology, invertebrate animals, fish, physiology and pollution research; also includes a most valuable list of limnological papers published in the British Isles in 1957.

Oundle School Natural History Society (1958). Report for 1957.

In addition to faunistic notes contains a survey of the rookeries of the district.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1958

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1958

Income

1957		£ s. d.	£ s. d.
	Subscriptions receivable:		
	(*Including* Arrears and *less* Payments in Advance):		
651	Members taking *Journal of Ecology* only	1057 1 9	
371	Members taking *Animal Ecology* only ...	561 15 10	
125	Members taking both Journals ...	532 18 9	
4	Associates	9 17 6	
		2161 13 10	
	Less: Reserve carried forward to 1959 for second part of *Journal of Animal*		
219	*Ecology*	406 0 0	
		1755 13 10	
	Add: Reserve brought forward from		
204	1957 for *Journal of Animal Ecology*,		
	Vol. 26, No. 2	219 0 0	
1436			1974 13 10
	Interest received:		
148	Investments	109 8 3	
11	Deposit Account	3 8 2	
38	Post Office Savings Account	2 13 6	
197			115 9 11
	Watson's Census Catalogue of British		
1	*Lichens*—Sales		5 0
	Biological Flora of British Isles—Sales less		
7	cost		19 5 4
2	*Index, Journal of Ecology, Vols. 1-20*—Sales		22 5 5
	Net Deficit for the year transferred to Balance		
5768	*Sheet*		1413 7 7
7411			£3545 7 1
	Journal of Ecology:		
	Sales:		
3502	Volume 46		3537 2 3
900	Back Volumes		519 7 1
1	Reprints of papers		— — —
98	Contributions for plates		— — —
	Loss on Journal transferred to Revenue		
6039	*Account*		2413 9 10
10 540			£6469 19 2

Expenditure

1957		£ s. d.	£ s. d.
	Working Expenses:		
89	Meeting Expenses	105 6 0	
27	Clerical Assistance	61 0 0	
18	Audit Fee	18 7 6	
5	Addressograph	5 1 6	
1	Bank Charges	10 8	
28	Postage	27 13 4	
21	Printing and Stationery	30 9 6	
23	Travelling	23 9 10	
212			271 18 4
	Grants and Subscriptions:		
	British Committee for Nature Conservation	10 0 0	
	Burren Research Fund	25 0 0	
	Council for Nature	2 2 0	
4			37 2 0
	Journal of Ecology:		
6039	Cost *less* Sales		2413 9 10
	Journal of Animal Ecology:		
872	Cost *less* Sales		229 2 10
284	*Loss on Sale of Investments*		593 14 1
7411			£3545 7 1
	Journal of Ecology:		
	Costs:		
	Printing, Paper, Blocks and Binding:		
6071	Volume 46		5117 18 8
	Binding Back Issues		26 3 0
3107	Reprinting Vols. 32, 35-38		— — —
920	Publisher's Commission		871 15 9
366	Carriage		451 14 3
76	Miscellaneous Expenses		2 7 6
10 540			£6469 19 2

	Sales:						
1662	Volume 27			1140	14	8	
1280	Back Volumes			1238	18	4	
5	Abstracts			3	14	2	
—	Notice of Publications			1	0	9	
	Loss on Journal transferred to Revenue						
872	*Account*			229	2	10	
3819			£	2613	10	9	

	Costs:						
	Printing, Paper, Blocks and Binding:						
2506	Volume 27, No. 1			989	18	3	
302	Binding Back Issues			318	15	0	
331	Reprinting Volumes 12 and 16 ...			787	2	11	
480	Publisher's Commission			425	19	8	
170	Carriage			91	14	11	
30	Miscellaneous expenses			—	—	—	
3819			£	2613	10	9	

BALANCE SHEET AS AT 31st DECEMBER, 1958

	Assets	£	s.	d.	£	s.	d.
	Cash at Bank						
	Westminster Bank Ltd.:						
713	Current Account	794	16	6			
100	Deposit Account	600	0	0			
813					1394	16	6
108	*Post Office Savings Bank Account* ...				110	6	6
32	*Income Tax recoverable from Inland Revenue*				25	10	0
	Publishing Accounts due from Publishers						
	Index Volume *Journal of Ecology* ...	22	5	5			
	Biological Flora	19	5	4			
208					41	10	9
	Investments at cost						
	£700 3% Savings Bonds	700	0	0			
	£1500 Federation of Rhodesia and Nyasaland 4% Stock 1972/74 ...	1519	3	0			
3935					2219	3	0
36	*Sundry Debtors*				5	14	8
5132				£	3797	1	5

	Liabilities				£	s.	d.
	Members' Subscriptions						
102	Paid in advance for 1959 onwards ...				33	1	6
1	*Library Fund*				1	5	0
—	*Burren Fund*				500	18	1
	Publishing Accounts owing to Blackwell Scientific Publications Limited						
2984	*Journal of Ecology*	2413	9	10			
—	*Journal of Animal Ecology*	30	2	2			
					2443	12	0
	Reserve of Subscriptions for 1958 (Allocated to second part of *Journal of*						
219	*Animal Ecology*)				406	0	0
	General Revenue Account						
	Surplus in Hand at 31st December, 1957	1825	12	5			
	Less: Net Deficit for the year ended 31st December, 1958	1413	7	7			
1826					412	4	10
5132				£	3797	1	5

We have examined the above Balance Sheet and annexed Income and Expenditure Accounts of the British Ecological Society as at 31st December, 1958. We have obtained all the information and explanations we have required, and have verified the Investments and Balance at Bank. In our opinion the above Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Society's affairs, according to the best of our information and the explanations given us, and as shown by the books of the Society.

F. H. WHITEHEAD
J. L. HARPER
Hon. Treasurers

RYLAND, CLIFT & MORRISON Incorporated Accountants
10 Eccleston Place, Westminster, London, S.W.1. 19 *March*, 1959

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed : **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Dates should be in the form '1 Jan. 1956, 25 June' etc., not 'Jan. 1st., or with the month indicated by a figure. Text-figures are to be referred to as 'Fig. 1', etc. In the use of symbols, signs and abbreviations *British Standard 1991 : Part I : 1954* should be followed, including the omission of all unnecessary full stops.

The *Journal*'s conventions regarding cross-headings should be followed, but they should not to be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form:

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7,** 303-4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals*, except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. OFFPRINTS. Authors are supplied with 50 offprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Offprints are sent out about a month after publication.

THE BRITISH ECOLOGICAL SOCIETY

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A. R. Clapham, D. E. Coombe, C. D. Pigott, P. W. Richards

The British Ecological Society was founded in April 1913, when it replaced the British Vegetation Committee (founded in 1904). The object of the Society is to promote and foster the study of Ecology in its widest sense. This it does by publishing the *Journal of Ecology* and the *Journal of Animal Ecology*, and by holding regular meetings when papers are read and symposia and discussions on subjects of current ecological interest are held. At present these meetings are held in early January, March or April, and September, in London, Oxford or Cambridge or a provincial centre. A fourth meeting in July is devoted primarily to field excursions from a convenient centre to places of ecological interest.

Membership of the Society is open to all, whether or not they reside in the British Isles, who are genuinely and personally interested in Ecology and wish to receive the Society's journals for their own use. The minimum subscription for membership is 40*s*., due on January 1st each year. This entitles members to receive *one* of the two journals, to attend the meetings and make use of other facilities that the Society may offer, to vote in the election of Council and Officers and be eligible for election to Council and Office. For a subscription of 70*s*. members may receive *both* journals. Membership does not include the right to any reduction in the price of back numbers of the journals, except those published in the year of election.

Associate Membership of the Society is open to those who wish only to attend meetings. Associates pay an annual subscription of 7*s*. 6*d*. and do not have the right to receive a journal or vote at a meeting of the Society.

Local Natural History Societies, Field Clubs and other similar bodies are eligible for a special membership of the Society.

Full details of membership and an application form may be obtained on request from either of the Honorary Secretaries.

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WORLD-LIST ABBREVIATION: *J. Anim. Ecol.*

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